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Vol. VI.

STUDIES

MORPHOLOGICAL LABORATORY

UNIVERSITY OF CAMBRIDGE.

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Vol. VI.

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On the Occurrence of Embryonic Fission in Cyclostomatous Polyzoa.

By

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With Plates I, II & III.

THE results of the present paper have formed the subject of a preliminary communication made to the Cambridge Philosophical Society (16). The case of embryonic fission which I have now to describe in greater detail appears to me, on the assumption that my explanation of the observed facts is the correct one, to be without parallel in the animal kingdom.

My observations refer entirely to the genus Crisia, and in particular to a form common at Plymouth, which I have described as a new species under the name C. ramosa (17). The general results may be stated as follows:—

(i) The ovicell, which is morphologically equivalent to a zoœcium, develops at the growing-point in the same way as an ordinary zoœcium.

(ii) A polypide-bud is found in the young ovicell, consisting of tentacle-sheath and a part which represents the alimentary canal of a polypide.

(iii) Small egg-cells are present in various parts of some of the growing-points. One of these acquires a close relation to the potential alimentary canal of the ovicell-polypide.

(iv) This potential alimentary canal grows round the ovum, losing its previous form, and becoming a compact multi-

nucleated follicle surrounding the egg, which at first lies in an excentric cavity in the follicle.

(v) The ovum segments[1] and the blastomeres may, in early stages, be completely separated from one another. The relations of the segmenting egg to its follicle are similar to those described by Salensky (28) in Salpa (cf. Salensky's figs. 12, 13, on pl. x).

(vi) The ovicell is meanwhile maturing, and by the end of the segmentation of the ovum has been shifted to some distance from the growing-point by the superposition of new zoœcia above it. Its non-calcified aperture, which, at an earlier stage, formed the wide end of a large funnel, has become constricted, and has grown out into a long tubular orifice.

(vii) At the end of segmentation, the embryo consists of a small mass of undifferentiated cells, lying near the distal end of the follicle, which has increased largely in size, and now forms a spherical knob projecting freely into the interior of a spacious tentacle-sheath. A complicated arrangement of cells connected with the aperture has meanwhile been formed.

(viii) The follicle becomes vacuolated, and is soon transformed into a nucleated protoplasmic reticulum. The tentacle-sheath loses its distinctness.

(ix) The number of blastomeres increases, cell-limits being indistinguishable at this, as at all other stages, excepting the very earliest.

(x) The embryo, having thus considerably increased in size, although remaining a solid mass, without differentiation of organs, grows out into several finger-shaped processes, which are generally directed towards the distal end of the ovicell.

(xi) The finger-shaped processes are divided up by a series of transverse constrictions into rounded masses of cells, each of which becomes a complete larva.

(xii) This process of embryo-formation continues during the whole functional period of the life of the ovicell, and is still actively proceeding at a stage when many of the embryos are mature, or nearly mature. The number of (secondary) embryos

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[1] The occurrence of a process of fertilisation was not made out.

present in an ovicell at any one time may exceed one hundred, and these have all been produced by budding from the above-described "primary embryo."

(xiii) Each of the "secondary embryos" acquires its well-known two-layered condition at the time of its separation from the budding mass of embryonic cells. It develops in a vacuole of the protoplasmic reticulum, which presumably supplies it with nutriment since the embryo rapidly increases in size, becoming ciliated externally, and ultimately escaping through the tubular aperture of the ovicell as a characteristic Cyclostome larva.

Taking the above history into consideration, it is not surprising that, as is actually the case, the Cyclostome larva differs considerably in structure from that of other marine Polyzoa. This history also explains the fact that no observer has ever succeeded in giving an account of any process corresponding to egg-cleavage in Cyclostomata.

The protoplasmic mass surrounding the embryos has been figured by Smitt (34),[1] who has alluded to the yellow colour so characteristic of the contents of the ovicell. This colour is contained principally in the protoplasmic reticulum, although the embryos themselves have a yellowish colour.

The first satisfactory account of the Cyclostome larva was, however, given by Barrois (1), who calls special attention to the fact that no previous observer had been able to discover "genital products" in any Cyclostome, and adds, "Je n'ai pour ma part encore réussi qu'à suivre les morulas jusqu'à des stades composés d'un nombre d'éléments de moins en moins nombreux et plus volumineux, sans réussir encore à constater d'une manière bien certaine la présence de l'œuf;" although supposing that the Cyclostomes do not really differ from other Polyzoa in this respect.[2] Barrois' failure to understand the early development of the embryos is readily explained if my own account be correct; and it is not surprising, con-

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[1] See his pl. iv, fig. 2.
[2] L. c., pp. 58, 59, note.

sidering the great difficulty of making out anything of the
nature of the early stages except by means of sections.

Barrois expressly states that the earliest stage to which he
succeeded in tracing his morulas with certainty is that repre-
sented in his pl. iii, fig. 3. This stage exactly corre-
sponds with the condition at which I have found the
embryos to be constricted off from the budding
primary embryo (cf. Pl. II, fig. 11). Barrois was, how-
ever, once successful in finding a cell, the egg nature of which
he considers uncertain (his pl. iii, fig. 1); and in another case
in finding what may have been an egg divided into two blasto-
meres. It is not easy to say whether the former cell was
really an egg, or whether it was merely one of the giant-cells
described below.

The rest of Barrois' account contains an erroneous history
of the later stages, which he himself was the first to correct
(2). I am compelled to doubt altogether Barrois' account
here given (not accompanied by any figures) of the supposed
occurrence of a process of segmentation of the egg, accom-
panied by the formation of an epibolic gastrula. In a later
paper (3) Barrois figures quite accurately the "morula" at
the stage at which it becomes independent (his pl. i, fig. 26),
although he wrongly supposes that the inner layer of cells
disappears in the later stages (his pl. iii, figs. 29, 30).

Although Metschnikoff (23, pl. xx, figs. 61—64) gives
admirable figures of the early embryos of Discoporella
radiata, the earliest stage observed by that author is the
stage at which the "secondary" embryo becomes free from
the budding mass of embryonic cells. Ostromnoff (25) is no
more fortunate in elucidating the early history of the embryo
of Cyclostomata.

I. Development of the Ovicell.

This process, which takes place fundamentally in the same
manner in all the species of Crisia which I have examined,
has been to some extent described by Smitt (34), although
most writers have paid little attention to the difference

between the form of the adult ovicell and that of the younger
stages of the same organ.

The ovicell is developed at the growing point, and it is here
that the early stages in the development of the egg take place.
A young internode[1] may be described as an acute-angled
isosceles triangle with two sub-equal sides (*AB, AC*). Within
the triangle a calcareous septum occurs parallel to *AB*, cutting
off the oldest zoœcium of the internode from the others.
The next septum is parallel to *AC*, and is nearer to the base
of the triangle. The formation of septa, alternately parallel
to *AB* and *AC*, gives rise to a series of alternate zoœcia, an
arrangement characteristic of Crisia. The oldest zoœcia are,
of course, those nearest to the apex of the triangle, and the
central part of the base is the region from which, with con-
tinued growth, fresh zoœcia are cut off. It remains to be
stated that the growing-point, like the adult internode, is
flattened, and that the openings of the zoœcia are lateral, and
are directed towards one of the flat surfaces of the branch.

As the internode elongates, its proximal zoœcia acquire their
full length, and cease to take part in the formation of the
growing-point. Or, explaining this by the former illustration,
let the internode grow to twice its former length, the growing
point remaining of the same width throughout its growth.
By producing the lines of the septa already present it will be
seen that if the growing point does not grow wider the older
zoœcia will be excluded from it, their growth being completed.
It follows that the zoœcia, several of which occur in a young
state at the end of the branch, become successively shifted to
the edges of the growing-point, preparatory to leaving it
altogether.

The growth of the zoœcia and of the ovicells takes place by
the apposition of fresh material at the distal end. The proxi-
mal end of each unit of the colony is first laid down, and the
last-formed portion is the aperture. Thus, by drawing a line
transversely at any level across an internode, whether the in-
ternode bears an ovicell or not, we obtain an accurate idea of

[1] Compare Pl. III, fig. 15.

the condition of the branch when the growing-point was at the
level of that line. It follows from the shape of the ovicell,
that an ovicell which is half grown will have the form of a
wide-mouthed funnel, as shown in the figures of Smitt and
others. But although it is easy to recognise a young ovicell
at this stage, it is anything but an easy matter to distinguish
the ovicell while it is still a sub-median member of the
growing-point.

The ovicell is indeed merely a modified zoœcium, as is
shown by the method of its development, as well as by its
internal structure. Further evidence for this statement is
afforded by the occasional occurrence of abnormal units of the
colony, intermediate in form between the zoœcia and ovicells
(17, pl. xii, fig. 12).

In Pl. III, fig. 19, the proximal portion of the ovicell is
already developed. The first, second, and third units of the
internode are zoœcia, the fourth being an immature ovicell.
The growing-point is formed, on the right side, by the base of a
lateral branch, which would have been borne by the fifth
member of the internode. There follow, in order from right
to left, the fifth unit, the actual growing-point capable of pro-
ducing fresh zoœcia, the sixth unit, and the ovicell. The last
occurs at the left side of the growing-point; but while its
proximal end is in the same plane with the zoœcia of the inter-
node, the open end of the funnel is already projecting forwards
(i. e. in the direction of that surface of the internode on which
the zoœcia open). This condition becomes more prominent at
a later stage, so that the ovicell, in its most swollen portion,
projects considerably beyond the level of the general surface
of the internode.

By referring to pl. xii, fig. 11, of my former paper (17) it will
be seen that the zoœcium "5" (in fig. 19) would have formed
its aperture at the level of the middle of the ovicell, while "6"
would have completed its growth at a very short distance
above it.

The young ovicell has, at first sight, the appearance of an
open funnel. This is not really its condition, since its end is

closed by a chitinous uncalcified membrane (ectocyst). This is the condition of the ovicell, and of the growing-points generally, at all stages before their growth is completed and the definitive apertures are formed. The funnel, which is, in fig. 19, the most conspicuous part of the ovicell, is consequently merely that part of the ovicell in which calcification has occurred.

In fig. 20 (in which the arrangement of the lateral buds does not correspond with that in fig. 19) the zoœcia have been numbered in such a way as to facilitate comparison with fig. 19. The zoœcium "5" is already complete, while "6" is beginning to free itself from the growing-point. The growth of the ovicell has progressed, the most swollen part is already completed, and the aperture (still closed by a membrane of uncalcified ectocyst) is beginning to constrict.

In fig. 21 the zoœcia "6" and "7" are complete. The aperture of the ovicell is still further constricted, and now consists of a slit-like portion which will soon close completely, and of a wider portion which will become the base of the tubular aperture so characteristic of this species (C. ramosa). A comparison of figs. 19—21 with one another will show that the method of the growth of the ovicell has been such as to bring its distal portion on to the front of the branch, while its proximal portion is lateral, and in series with the zoœcia. The base of the tubular aperture thus comes to be situated at about the middle line of the internode.

The valve of the ovicell (17, pl. xii, fig. 10) is formed as a ridge from the back of the ovicell at a stage between figs. 20 and 21. The growth of the ovicell will be completed by the outgrowth of the tubular aperture.

So far as I have been able to make out, the aperture is closed by the uncalcified membrane of ectocyst at all stages of its development, and does not become actually perforated until the escape of the first larva. I am quite unable to say when and how the process of fertilisation is effected.

II. The Male Sexual Elements.

There can, however, be no doubt of the existence of spermatozoa in Cyclostomes, although I am not aware that they have previously been described.

In Crisia I have usually found them in colonies without ovicells[1] (17, p. 145), although they occur in ovicell-bearing colonies in Idmonea serpens.

The spermatoblasts occur in masses filling up a large portion of the body-cavity of sexual individuals. The sperm mother-cells in both Idmonea and Crisia seem to occur in groups of four (Pl. I, fig. 4); and the four flagella when first developed appear, under insufficient magnification, as if they belonged to one cell. The mature spermatozoon (fig. 4) possesses an elongated head (measuring about ·0064 mm.), and a long, active flagellum.

In C. cornuta it was noticed that a delicate, hyaline layer of endocyst protruded from the aperture of the zoœcium, during the escape of the spermatozoa, in the form of a cone at the apex of which the spermatozoa escaped.

III. The Origin of the Secondary Embryos.

My observations on this part of the subject have been made almost entirely by means of sections. The ovicells were preserved and decalcified, at one operation, by placing in a mixture of corrosive sublimate, nitric and acetic acids. The most successful staining was obtained with Grenacher's hæmatoxylin or with borax-carmine, in the latter case washing with alcohol containing picric acid.

The free larva of C. eburnea is well figured by Barrois (1, pl. iii, fig. 22). It is, roughly speaking, cylindrical in shape, being covered externally by a complete coating of cilia. At one end of the cylinder is an aperture leading into the "sucker," by means of which fixation is effected; and, at the opposite end, is another aperture leading into the so-called

[1] In one case, spermatozoa were found in a colony of C. cornuta, which bore a single very young ovicell.

"mantle-cavity." I have observed no trace of a "pyriform organ." Barrois (2, p. 142; 3, p. 48, pl. iii, fig. 31) states, however, that he has discovered a rudiment of this structure in the larvæ of Discopora.

The internal structure of a young larva may be illustrated by means of fig. 23, a median longitudinal section. The sucker is already well developed, having been formed, as in most other Ectoproct larvæ, by a process of ectodermic invagination. Cilia have appeared on the greater part of the external surface, the non-ciliated part of the ectoderm representing the portion which will be later invaginated to form the mantle cavity. The inner layer of cells is still perfectly distinguishable, forming a thin layer, closely applied to the ectoderm, and enclosing a cavity which occupies the whole of the interior of the embryo.

The earlier stages, which alone concern us at present, may be realised by assuming that the volume of the embryo shown in fig. 23 has become largely reduced; and that the sucker has become flattened out. Slightly anterior to the stage of fig. 22, the sucker is much shallower, and opens by a wide aperture in the middle of the " oral " surface. Still earlier, the sucker is a very slight depression of the thickened "oral" ectoderm. The inner layer is at this stage a layer of great tenuity, in which a nucleus is thick enough to form a swelling wherever it occurs. Before this, the embryo is planoconvex, the position of the future sucker being represented by its flat side; and, still earlier, it is rounded in section, the inner layer consisting of a few cells, completely surrounding a central cavity. Between this stage and that shown in fig. 22, the inner layer may be separated, in parts or completely, from the ectoderm; so that it would be impossible to overlook its presence in any well-preserved section.

At the earliest stage at which the embryo is free in the ovicell, it consists of a small rounded mass (Pl. II, fig. 11) The outer layer is in the form of a continuous mass of protoplasm, enclosing one layer of nuclei. The inner layer also consists of continuous protoplasm, with a very small number

of nuclei arranged in one row; and it encloses a minute central cavity.

Pl. III, fig. 17, represents a median section, slightly magnified, of an ovicell of Crisia ramosa. The ovicell contained in all about 115 embryos, which were embedded in a loose protoplasmic reticulum, filling up most of the cavity of the ovicell. In the older embryos, the conspicuous sucker or "internal sac" is clearly seen; and in some of them, a slit-like space which is the mantle-cavity. The aperture of the latter to the exterior is not shown in any of these embryos. To the left of the ovicell is the structure from which all the embryos have been produced. This structure is labelled " primary embryo;" the evidence that this name implies its real nature being given in the sequel. The primary embryo is produced into several processes; and indications are seen, in at least one case, that the end of the process is being constricted off, as a rounded mass of cells, which is equal in size to the smallest of the embryos found free in the protoplasmic reticulum.

Fig. 11 (Pl. II) is a longitudinal section of a young ovicell, at the period when the formation of "secondary" embryos (i. e. embryos which are developed by budding from the "primary" embryo) has just commenced. The protoplasmic reticulum includes one or two free embryos, the structure of which has already been described. The most conspicuous structure in the section is, however, the large primary embryo, which consists of a dense mass of granular protoplasm containing numerous nuclei, and having an extremely embryonic appearance. This structure is in a state of active growth, as is shown by the occurrence of nuclei with karyokinetic figures. The proximal end of the primary embryo is compact and rounded, and contains centrally a group of nuclei which are distinguished by the activity with which they are undergoing division. The opposite end of the primary embryo is produced into several irregular processes, which show constrictions at intervals. From the ends of two of these processes, embryos have just been constricted off, and

are seen disconnected from the primary embryo. The con-
strictions indicate the limits of as many future embryos.

The "primary embryo" contains, distally, an irregular
cavity. It is difficult to be sure of the exact arrangement of
the embryogenic processes; but in some cases at least it is
evident that the distal end of the primary embryo has the
form of an irregular cup, the processes forming the wall of the
cup, from which they become free at their ends. The irre-
gular cavity seen in fig. 11 is part of the cavity of the cup.

Towards the ends of the processes an ectodermic layer
becomes clearly differentiated; while, in the centre of each of
the swellings indicating a future embryo, a small group of
inner-layer cells can, in some cases, be clearly distinguished.
The ectoderm of the processes is continuous with the outer
nucleated layer of the primary embryo, and with the similar
layer immediately lining its distally-placed cavity. The inner-
layer cells of the secondary embryos are continuous with the
inner nuclei of the more solid, proximal half of the primary
embryo. But these nuclei and the protoplasm surrounding
them are not throughout clearly differentiated from the outer
layer of nuclei. I am, however, inclined to suppose that the
somewhat triangular, clear mass of protoplasm at the proximal
end of the primary embryo, containing actively dividing nuclei,
is the region which gives rise to the inner-layer cells. This
region can generally be distinguished with ease in ovicells at
this stage.

The primary embryo consists of a mass of embryonic cells
(or, rather, nuclei embedded in continuous protoplasm) which
are obscurely differentiated into outer and inner cells (or
nuclei). The whole function of this embryo is to act as an
embryogenic organ, or producer of secondary embryos, and it
possesses no structures which can be described as its own
organs.

At its proximal end, the primary embryo is budding off
nuclei which migrate into the protoplasmic reticulum, where
they become indistinguishable from the rest of the nuclei
of that reticulum. I have been unable to make out the

significance of this phenomenon, which I have frequently observed.

I am in a position to multiply indefinitely figures showing the important fact that the young larvæ are really produced as buds from a " primary embryo." I consider that I have the clearest possible evidence of the following statements:

i. The larvæ are produced as buds from an embryonic mass of cells found in the young ovicell.

ii. They are produced in no other way than that mentioned under i.

The embryogenic organ is invariably present in all ovicells in which young embryos are found, and in most of the older embryo-containing ovicells as well. It is still active, even at the stage shown in fig. 17. The youngest embryos, free in the reticulum, are invariably identical in structure with the ends of the processes of the primary embryo, and there is not the slightest trace in any of the ovicells, young or old, of the development of larvæ by the ordinary process of the segmentation of an egg.

It might, indeed, be supposed that the bi-nucleated cell shown in the upper part of the reticulum in fig. 11 had the nature of a dividing egg. This supposition is not confirmed by an examination of the actual facts. While the evidence in favour of the origin of the larvæ by a process of budding is unmistakably clear, there are no transitions between such cells as the large one shown in fig. 11 and the young two-layered larvæ. These large cells, which are normally present in the ovicells, are probably of the nature of " giant-cells," similar to those which are found in developing bone. This subject will be considered later; but it may be pointed out that it is possible that the supposed egg-cell figured by Barrois (1, pl. iii, fig. 1) may have been one of these giant-cells.

IV. The Development of the Primary Embryo.

Fig. 15 (Pl. III) is a decalcified internode of C. eburnea, possessing a very young ovicell. The internode consists of one complete zoœcium, which bears the beginning of a lateral

branch; of a second zoœcium, which is very nearly mature; of the ovicell as the third member of the internode; and of the real growing-point, which contains a young polypide-bud; although the corresponding zoœcium is not yet separated off from the growing-point by a septum.

The ovicell contains a structure which is the exact equivalent of an ordinary polypide-bud. This consists of (1) a thick (proximal) mass of cells, which in a zoœcium would give rise to alimentary canal and tentacles; (2) a thin-walled portion, next to the above, and corresponding to the tentacle-sheath; and (3) a distal portion, indicated by two parallel lines in the sketch, and which is really an invagination of the distal body-wall of the ovicell. This is formed in a precisely similar manner in any young zoœcium, where it develops into the aperture.

Fig. 1 (Pl. I) is a nearly median longitudinal section of an ovicell at nearly the same stage as fig. 15. The body-cavity is, as in ordinary zoœcia, largely filled up by funicular tissue, but contains an obvious polypide-bud, the distal portion of which can be clearly distinguished as a tentacle-sheath, similar in all respects to the same structure in an ordinary polypide-bud. The one fact, indeed, which enables this member of the colony to be distinguished as an ovicell is the presence of a relatively large cell, which is closely applied to one wall of the polypide-bud. The latter shows some tendency to give off cells which are growing round the large cell. This has a diameter of about ·0176 mm., and it has a large clear nucleus with one or two nucleoli. Its structure, in fact, reminds one irresistibly of that of an egg; and I believe this cell to be the source from which all the larvæ produced in the ovicell are developed.

. "Eggs" of this kind are found in various positions in some of the growing-points. Thus in the particular individual in question there is a second, smaller egg[1] in the same ovicell; and in the next zoœcium there are two eggs[1], one of which is at the apex of the polypide-bud. The fact that these eggs are commonly found in the growing-points leads me to suppose

[1] Not visible in the particular section figured.

that several are produced in each fertile internode, apparently
by a modification of cells of the funicular tissue, and that their
further development depends on their entering into definite
relation with a polypide-bud. If this association is brought
about, it may be assumed that what might at first have de-
veloped into a zoœcium becomes an ovicell. In abnormal
cases, where several polypide-buds enter into relation with
ova, two or more ovicells may be produced in the same inter-
node (17, p. 166; pl. xii, fig. 13). It may further be sup-
posed that the failure to bring about the association between
the egg and the polypide-bud results in such abnormalities as
that shown in fig. 12 of my former paper, and that this or some
other cause, such as the failure to get fertilised, results in the
development of the empty ovicells which are so frequently
observed.

On decalcifying a number of ovicells, it is soon noticed that
many ovicells are either completely empty or are abnormally
developed. An ovicell, with complete tubular aperture, may
be absolutely devoid of any trace of primary or secondary
embryos. In some cases, these empty ovicells are probably
the result of degeneration which has set in after the comple-
tion of the process of development of free larvæ. After the
escape of the last larvæ, the remaining tissues of the ovicells
degenerate, and are gradually absorbed. Many of my sections
bear out this assertion.

In other cases, however, the degeneration takes place in
ovicells which have produced no larvæ. Empty ovicells which
are near the growing-points are, probably, generally of this
character. It is easy to obtain evidence of the fact that, in
such cases, degeneration may set in at various periods—some-
times after the egg has developed to a considerable extent.
In some cases, this may be the result of the absence of fertili-
sation—a process of which I have vainly endeavoured to prove
the existence. That fertilisation does actually occur at some
period can hardly be doubted, considering the fact that normal
spermatozoa are developed in some colonies. In other cases,
the degeneration is probably due to the atrophy of the poly-

pides in the zoœcia contiguous to the ovicell. It is well known that the thick calcareous ectocyst of the Cyclostomata is perforated by pores. On decalcifying a colony, and staining what is left, it can be easily shown that all the zoœcia are in organic connection by means of the funicular tissue, which passes through the pores from one zoœcium to another, and from the zoœcia to the ovicell. It can hardly be doubted that the nutriment at the expense of which the larvæ develop is provided by means of the protoplasmic network which thus connects all the individuals of a colony. The ovum is extremely minute, although it gives rise to a massive primary embryo; and this to numerous free larvæ, each of which is very many times larger than the original ovum. This rapid growth—to say nothing of the development of an extensive reticulum of funicular tissue in the ovicell itself—can only depend on the existence of pores by which the ovicell is connected with zoœcia which possess functional polypides.

In fig. 2 the ovum is completely surrounded by the polypide-bud, whose tentacle-sheath has considerably increased in size; while in fig. 3 further alterations of importance have taken place. The tentacle-sheath has grown very much larger; but, so far as this structure and the invagination which forms the aperture are concerned, the ovicell still resembles an ordinary zoœcium. The proximal part of the polypide-bud, which in the younger ovicell was practically indistinguishable from the corresponding structure in an ordinary zoœcium, has now become much modified. The egg is now completely surrounded by it; and the polypide-bud has in fact transformed itself into a round mass of cells which may be termed the "follicle." The ovum lies partly surrounded by a cavity in this follicle.

The fact that the distal endocyst is not in contact with the ectocyst is probably due to shrinkage brought about during decalcification. The side-walls of the zoœcium are of course calcified (cf. fig. 19), while the distal ectocyst forms an uncalcified membrane stretching across the mouth of the funnel formed by the ovicell.

It is presumably at this stage that fertilisation takes place; but I have in vain looked for any evidence of perforation in the terminal membrane of the ovicell, or for traces of spermatozoa inside the tentacle-sheath. This fact is not really surprising when it is remembered that the finer details of the highly calcified ovicell of Crisia can hardly be examined except by means of sections; and that the spermatozoa are very minute.

In fig. 5 the whole ovicell has considerably increased in length. Its irregular form is of course due to shrinkage caused by the action of reagents. The ectocyst is not represented in the figure. The ovicell was probably at about the stage represented in fig. 21.

The valve (cf. pl. xii, fig. 10, of my former paper) is now developed as a fold of the ectoderm on the back wall of the ovicell. The aperture has no longer any obvious opening to the exterior; and the tentacle-sheath has increased in size, its walls having become very thin, except at its distal end, which is considerably thickened.

The follicle is slightly larger than before, and its nuclei have obviously increased in number. In place of the egg found in the preceding stage, there are now three egg-like cells, which are not in contact with one another; and which I regard as blastomeres. Remains of the follicle-cavity are still present.

Although I have no direct evidence that the "blastomeres" are really derived from the egg, their subsequent history leaves room for little doubt on this point. The details of the formation of the primary embryo in Crisia remind one strangely of the early development of Salpa, as described by Salensky (28). This is true not merely of the segmentation of the ovum, but also of the later relations of the embryo to its follicle. Salensky states, for instance, that the blastomeres of Salpa may at first be entirely disconnected from one another (l. c. pl. x, fig. 10; pl. xxii, figs. 3, 4).

In the next stages, of which I have numerous preparations, but which I have not figured, the number of blastomeres gradually increases. I have been unable to make out any regu-

larity in the succession of the blastomeres, which are, in fact, inextricably entangled among the follicle-cells. They are not necessarily in contact with one another, but may be separated from one another by ingrowths of the follicle-cells, so that in most preparations it is almost impossible to count the number of the blastomeres, or to distinguish all of them from the follicle-cells. An excellent idea of the general relation of the blastomeres to the follicle-cells (or nuclei) may be obtained by referring to some of Salensky's figures of Salpa, as his pl. x, figs. 12, 13. The only difference that I can point out between Crisia and Salpa, as regards the relation of the blastomeres to the follicle-cells, is that in Crisia the follicle is somewhat larger relatively than in Salpa, and that the blastomeres occupy only the central region of the follicle instead of filling up most of that structure, as in Salpa. Remains of the follicle-cavity may still be detected in some of these stages.

In fig. 6 (which is connected with fig. 5 by numerous preparations, forming a perfectly continuous series, in my possession) the tentacle-sheath has increased in size so much as to fill up nearly the whole of the ovicell. The follicle has largely increased in size, and now forms a sub-spherical knob, projecting freely into the cavity of the tentacle-sheath. This stage is a perfectly constant and easily recognised one.

The scattered blastomeres have at last come together to form a small but compact embryo, in some of the nuclei of which karyokinetic figures are discernible. There is no trace of the differentiation of germ-layers in the embryo, which consists simply of a small rounded mass of undifferentiated embryonic cells, or rather of a continuous mass of protoplasm, containing nuclei scattered through it without any attempt to arrange themselves in definite layers.

At the distal end of the embryo is a clear part of the follicle which contains small nuclei. This is apparently a constant feature of the stages near this one; but I have not been able to make out its significance.

Fig. 7 is not cut quite medianly, so that it does not show that the attachment of the follicle to the tentacle-sheath is

much the same as in the former figure. The tentacle-sheath is, however, now becoming less definite. To the left of the figure it is hardly distinguishable from the follicle, with which it probably fuses.

.The embryo is practically unaltered, except that it has come to the surface of the follicle; but the principal difference between this and the earlier stage concerns the follicle itself. This structure no longer forms a compact mass of granular, nucleated protoplasm, as in fig. 6; but it has become distinctly vacuolated. This vacuolation is the beginning of the process by which the follicle of earlier stages is transformed into the protoplasmic reticulum of later stages.

Fig. 9 (Pl. II) well illustrates the manner in which this transformation is effected. The tentacle-sheath is not so clear as in the former stage, and can, indeed, hardly be distinguished except at its upper end. Whilst in earlier stages it filled up most of the ovicell, it has now collapsed to a large extent.

The proximal portion of the follicle is in this ovicell still solid, and is perfectly similar in structure to the solid follicle of fig. 6. Distally the follicle is almost unrecognisable, having become separated by enormous vacuoles into strands of anastomosing, nucleated protoplasm. These strands are, however, most unmistakably continuous with the proximal, solid portion of the follicle. The embryo is practically unaltered, still forming a small rounded mass of undifferentiated embryonic tissue lying in a part of the reticulum.

The great increase in the size of the follicle and in the number of its nuclei up to the stage shown in fig. 11 is probably connected with the development of a nutritive arrangement for the young larvæ. The minute egg-cell of fig. 1 gives rise, as I believe, to the embryogenic organ of fig. 11, and this to the numerous young larvæ with which the mature ovicell is crowded. These larvæ lie in the meshes of the protoplasmic reticulum, from which they are probably supplied with nutritive material.

In figs. 6 and 9 the base of the ovicell has a very characteristic structure, always noticed in young ovicells at certain stages.

Next to the ectocyst comes a very definite nucleated layer, which encloses a network of cells separated by smallish vacuoles.

In later stages the outer definite layer of nuclei disappears, and the network becomes continuous with the reticulum formed by the modification of the follicle (fig. 11). The basal network of cells is obviously part of the ordinary funicular tissue, which, as has already been pointed out, forms a continuous connection from zoœcium to zoœcium, or from zoœcium to ovicell, through the pores in the calcareous septa between neighbouring individuals. It can hardly be doubted that the rich protoplasmic reticulum in which the young larvæ lie is the means by which nutriment is conveyed to the developing larvæ.

Fig. 10 is a stage of which I obtained only one example, and I cannot be sure that what is there represented is really a normal process. This preparation indicates that a kind of invagination takes places in the embryo at this stage (which is certainly very near that shown in fig. 9). If this is really correct, the inner layer of the primary embryo may possibly be formed by a process of invagination, and the inner layer of the secondary embryos is then probably derived from this invaginated layer; but I make these suggestions with all reserve.

Fig. 8 is interesting partly because it supports the view advanced in my former paper (17) that the species there described as C. ramosa is not identical with C. eburnea. The figure is a longitudinal section of an ovicell of C. eburnea; and so far as the general development of the ovicell goes, the age corresponds with the stage shown, for C. ramosa, in fig. 6.

The tentacle-sheath is at its period of maximum development; but the relative sizes of follicle and embryo are widely different from their relative sizes in C. ramosa. This appears to be a constant difference between the two species. In C. eburnea, the follicle is reduced to a minimum, and the quantity of the protoplasmic reticulum of mature ovicells is,

consequently, appreciably smaller than that in C. ramosa, although in old ovicells of the latter species even, the quantity of the protoplasmic reticulum may be considerably reduced, by the development of the larvæ at its expense. The primary embryo, on the contrary, is relatively very large. It has differentiated a distinct external layer of nuclei, which will give rise to the external layer of the secondary embryos. Throughout the development, the budding secondary embryo of C. eburnea differs considerably from that of C. ramosa; although the fundamental facts are the same in both species.

I have, unfortunately, no satisfactory sections of the ovicells of other species, which I found more difficult to obtain than the two former species. It is necessary to have a large stock of material in order to study the development; as it usually happens that a very small proportion of the colonies found are provided with ovicells.

The stages intermediate between figs. 9 and 11 have not been figured; but it is easy to describe their general development. After the stage shown in fig. 9 (but not until then) the embryo increases in size, and rapidly transforms itself into the characteristic mass of embryonic cells from which the young larvæ are budded off.

The history of the aperture of the ovicell has, so far, not been considered in sufficient detail. Its commencement as an invagination of the endocyst has been seen in fig. 3. When the egg has begun to segment (fig. 5), the opening of the invagination has closed. The distal end of the tentacle-sheath is, however, now thickened; and the valve is commencing to develop.

In fig. 8 (C. eburnea), the valve is practically complete; the distal thickening of the tentacle-sheath has increased, but the invagination constituting the primary aperture has not materially altered. The ovicell is completely calcified except in the region of its aperture, which is beginning to grow out into its tubular form. This part is covered merely by uncalcified ectocyst.

Fig. 12 represents a slightly earlier stage in C. ramosa.

The primary aperture is still present; the distal thickening of the tentacle-sheath being already distinct, and showing a differentiation of an external epithelial layer, and a more internally placed mass of nucleated protoplasm.

It is very difficult to make out with certainty the later history of the aperture. In stages previous to that at which the solid follicle has its maximum size, the connection of the primary aperture with the distal wall of the ovicell seems to be completely lost in many cases. It is perhaps the case that the original invagination remains connected with the distal wall of the ovicell by a thin cord of cells which is not easily seen in sections—accounting for the apparent discontinuity between endocyst and apertural invagination which is frequently remarked; and that, later, this cord shortens, bringing the invagination once more nearer to the distal wall of the ovicell, where its aperture once more opens out widely.

In fig. 13, representing the aperture of an ovicell in which traces of vacuolation are beginning to appear in the follicle, the primary aperture still opens to the exterior; although, in accordance with what has just been said, its opening would probably not have been discernible at a somewhat earlier stage. The formation of the tubular definitive aperture has progressed, and the valve is complete. The differentiation of the thickened part of the tentacle-sheath into two kinds of cells, alluded to in the description of the last figure, has advanced a stage.

In fig. 9 the tubular aperture is practically complete. At its end is seen an invagination which I regard as the remains of the primary aperture, but which has now become disconnected from the thickened part of the tentacle-sheath.

The history of the aperture is thus, according to what I believe I have made out, as follows :—During the calcification of the distal end of the ovicell, the primary aperture, which at first opened in the middle of the mouth of the funnel, becomes shifted nearer the " back " wall of the ovicell, into the position where the tube of the ovicell is to be formed. The aperture is thus not closed by the calcification of the ovicell, but finally

disappears in the region of the permanently uncalcified part of
the ovicell; i.e. of the definitive aperture.

Fig. 14 illustrates a condition of the tube of the ovicell
which I have observed in one or two cases. The ectocyst is
drawn out into a long narrow tube, which was probably un-
calcified and which opens to the exterior. This recalls the
condition described in the zoœcia of certain Cyclostomata, in
which the zoœcium is closed by a (calcareous) lid, perforated
by a small central aperture.[1] I am not prepared to state
whether or not this is a normal character of ovicells at any
particular stage, nor can I suggest any satisfactory explanation
of the meaning of the phenomenon.

The central mass of cells differentiated from the thickened
part of the tentacle-sheath in fig. 12 is destined to undergo
certain very important modifications. In fig. 16 (more highly
magnified than the previous figures, and belonging to the same
ovicell from which fig. 6 was drawn) some of the nuclei of the
central mass are growing larger. This is especially the case
in the neighbourhood of the lumen of the tentacle-sheath,
where there is a tendency for the nuclei to group themselves
in small numbers. In fig. 9 some of these multinucleated
masses of protoplasm are breaking off into the lumen of the
tentacle-sheath.

From this stage onwards the characteristic multinucleated
cells, which have been formed from the thickened distal part
of the tentacle-sheath, are a normal feature of the ovicell, being
found in the vacuoles of the protoplasmic reticulum in which
the young larvæ lie. One of them is seen in fig. 11, and
others are shown, more highly magnified, in fig. 18 (Pl. III).
In the latter figure the multinucleated cells contain nuclear
and other structures which are obviously degenerating; and
they are clearly not unlike the "giant-cells" which are known
to occur in certain tissues in Vertebrates.

The giant-cells make their appearance at just that stage

[1] Cf. Mesentipora meandrina (Busk, No. 8, pl. xvii, fig. 2); Reticu-
lipora dorsalis (Waters, No. 36, pl. xvii, fig. 4); and other cases referred
to by Waters.

when the vacuolation of the follicle is commencing; and they appear to be closely connected with the carrying out of this process of vacuolation, although it is clear that the first small vacuoles (cf. fig. 7) make their appearance independently of the giant-cells.

At later stages each giant-cell is usually seen to lie in a large, sharply-marked vacuole of the protoplasmic reticulum. The cell may be apposed to one wall of the vacuole; or may, apparently, lie quite freely within it. There is good reason to believe that the vacuoles which are at first occupied by giant-cells are later occupied by the young larva. Each embryo, soon after its formation, comes to lie in a sharply-marked vacuole in the protoplasmic reticulum. Taking into consideration the facts (1) that the giant-cells are formed simultaneously with the appearance of large vacuoles in the follicle, and (2) that they contain fragments of degenerating cells or nuclei, it may be concluded that one of the functions of the giant-cells is to excavate spaces in the follicle in which the larvæ can develop. These spaces are probably filled with some albuminoid fluid, at the expense of which the embryos develop —probably by diffusion through their tissues, as they have no recognisable means of absorbing nutriment.

The function of the giant-cells would thus be closely similar to that of the osteoclasts or myeloplaxes of bone " which excavate small shallow pits . . . . in the part which is undergoing absorption" (27, p. 104). Their structure, too, is in accordance with the descriptions of various observers of the multinucleated giant-cells in Vertebrates.

In the mature ovicell the remains of the distal thickening of the tentacle-sheath are always found as a dense mass of nucleated protoplasm which is attached to the ectocyst, not in the tubular aperture of the ovicell, but invariably at its base, on the side which is further from the back of the ovicell (figs. 9 and 16). The valve constantly projects from the back of the ovicell into the proximal part of this mass of cells in the manner shown in figs. 9 and 16. It appears to me probable that the function of the valve is to offer an obstacle to the

escape of the immature larvæ. When mature, the larvæ force
their way one by one through the solid mass of protoplasm
into the tubular aperture, and so escape to the exterior.

The tentacle-sheath is no longer easily distinguishable in
the mature ovicell. With the commencement of the vacuola-
tion of the follicle its distinctness vanishes, and it becomes
confounded with the vacuolated follicle. The relations shown
in figs. 9 and 17 probably indicate that the follicle ultimately
fills up the whole of the original tentacle-sheath, and that that
part of the ovicell which is not occupied by the protoplasmic
reticulum and its contents is the original body-cavity of the
ovicell.

The ovicells which are at their period of greatest activity can
readily be recognised in the living condition by the pronounced
yellow colour of their contents. This is sufficiently distinct
to show clearly through the calcified wall of the ovicell.
Although the embryos and larvæ are pale yellow, the colour
of the ovicell depends mainly on the pigment in the reticulum
which supports the embryos. In C. cornuta this is bright red-
orange in colour, while in C. ramosa the orange colour is not
quite so bright.

The oldest larvæ, which are almost ready to escape, lie each
enclosed in a distinct vacuole of the reticulum, in close contact
with the thick mass of protoplasm which fills up the aperture
of the valve.

The production of embryos continues up to a very late stage,
but embryos are always developed only from the budding mass
of embryonic cells (primary embryo). The budding organ has,
however, a somewhat different appearance in old ovicells
from that which it first had, both the secondary embryos and
their nuclei being markedly smaller than in the younger
ovicells.

So far as my observations go, the whole of the budding
organ is ultimately used up in the production of embryos. In
ovicells which are nearly exhausted the embryos are few in
number, and the budding organ has been reduced to small
dimensions. Finally, the ovicell is found to consist merely of

a protoplasmic reticulum, which may be richly developed, and which no longer contains any embryos or larvæ.

It must not, however, be assumed that all ovicells in this condition have passed through an embryo-producing stage. I have repeatedly obtained evidence to show that degeneration of the ovicell may start at almost any stage in its development. The external form of the ovicell may develop completely, even if the embryo and its follicle are degenerating. It is common to find an ovicell which, from its proximity to the growing-point, should be a young one, but which appears completely empty in sections. I can only assume in these cases that the protoplasmic structures which the ovicell at first possessed have been absorbed through the pores into the neighbouring zoœcia. In other cases the ovicell may contain remains of a degenerating follicle, the degeneration having clearly commenced before the follicle became vacuolated. One may, therefore, distinguish between a " primary" degeneration of the ovicell occurring before any larvæ have been produced, and a " secondary" degeneration, which has taken place after the escape of the last larva. It is sometimes possible to distinguish between these two conditions by reason of the fact that the base of the young ovicell is limited by a marked epithelial arrangement of its endocyst (cf. figs. 6 and 9).

I have so far avoided the use of the term "endoderm" as an equivalent for the inner layer of cells of the secondary embryos. This layer is excessively distinct in the embryos soon after their liberation from the embryogenic mass of cells. It then forms an epithelium, lying more or less close to the inner surface of the ectoderm-cells, and completely surrounding the whole internal cavity of the embryo (fig. 22).

In later stages the distinctness of the cavity becomes lost, and its lining cells send off processes which grow across the cavity and convert it into an irregular set of spaces. At the sides of the sucker these spaces disappear altogether, while between the sucker and the middle of the aboral pole the cavity remains distinct for a time longer. Its cells become, however, almost indistinguishable from the epithelium of the

sucker on the one hand, and from the epithelium lining the mantle-cavity on the other.

I formerly assumed (15, p. 455), on the authority of Ostroumoff's statements (25, pl. vi, fig. 1), that the cavity lined by the inner cells represented the alimentary canal of the larva. But, taking into account the manner in which the larvæ are developed, it appears to me doubtful whether any representative of the endoderm occurs in them. It appears to me to be satisfactorily established that a young polypide-bud in any Polyzoon is developed at the expense of two layers, viz. the ectoderm and a layer of funicular tissue which may be regarded as mesoderm.[1] The metamorphosis of the larva of Cyclostomata has been described by Barrois (3) and by Ostroumoff (25). The observations of Barrois show that the processes of fixation and of metamorphosis take place essentially as in other Gymnolæmata. The larva fixes by the eversion of its sucker, its mantle being rolled downwards so as to come into contact with the flattened plate formed by the eversion of the sucker, and the greater part of the larval tissues undergo a process of histolysis. The larva thus enters into the condition of a zoœcium containing a "brown body," and the young polypide is produced by an invagination of the body-wall from the centre of the surface opposite to the basal surface. While the inner layer of the bud is formed by an invagination of the ectoderm, Barrois was unfortunately unable to trace the history of its outer layer.

Ostroumoff is but little more definite on this point. The inner layer of the bud is formed, according to this observer, not as an invagination, but as a plate of cells split off from the aboral ectoderm. The edges of this plate curve round, so as to transform the plate into a sac, to the outer side of which "mesenchym-cells" apply themselves, and form the outer layer of the bud. The origin of these "mesenchym-cells" is not traced. It is recognised that the "alimentary canal" of the earlier stage disappears, but there is nothing to show how its cells are related to the "mesenchym-cells" shown in

[1] Cf. especially Seeliger, Nos. 32 and 33.

Ostroumoff's pl. vi, fig. 2, which, by the way, are unlike any cells which I have ever seen in a Cyclostome larva.

Whatever be the origin of the outer layer of the bud which which forms the primary polypide, it is quite clear that that polypide is formed in fundamentally the same way as any other polypide in the future colony. There can be no question of the "alimentary canal" of the embryo passing over directly into that of the primary zoœcium.

In default of sufficient evidence on this point I am inclined to regard the inner layer of the Cyclostome embryo as mesodermic rather than endodermic, and this principally on the following grounds :

1. The alimentary canal is an excessively rudimentary structure in the great majority of known Ectoproct larvæ.

2. The peculiar character of the early development of Crisia suggests that a representative of this rudimentary structure is likely to be found in the primary embryo only, and that the secondary embryos, formed by budding from the primary one, are no more likely to possess an alimentary canal than is a young zoœcium formed at the growing-point of an old colony.

3. The analogy of other Ectoprocta is in favour of this hypothesis.[1]

Prouho (26), for instance, has given an account (which I can confirm in the main from my own observations) of the metamorphosis of Flustrella. Even before the end of larval life, a distinct aboral mesodermic layer is present, from which the outer layer of the bud is directly developed.

In the course of the budding of an ordinary Ectoproct colony the polypide buds are formed from two distinct layers. The inner layer of the bud is developed at the expense of the ectoderm; the outer layer, either from an already definite layer of mesoderm (Phylactolæmata), or from mesoderm-cells of the funicular tissue which arrange themselves as an epithelium round the outside of the ectodermic portion of the bud

[1] Cf. particularly the larva of the Phylactolæmata, as described by Braem (5) and by Davenport (8A).

(most Gymnolæmata; cf. especially Seeliger, No. 38). There is no sufficient reason for supposing that a young zoœcium consists of anything but ectoderm and mesoderm. The Ectoproct larva may be considered morphologically as a young zoœcium containing a potential " brown body" (the remains of the purely larval organs), and it is not unreasonable to suppose that the structures found in the larva of the Cyclostomata, developed as it is by a process of budding, are comparable with those which are found in a zoœcium.

We arrive, therefore, at the provisional conclusion that the inner layer of the Cyclostome embryo is more likely to represent the mesoderm than the endoderm of the larva.

There can be no doubt that, on the assumption that my account of this process is in the main correct, the development of Crisia takes place in a manner to which there are few known parallels.

The most frequently quoted case of embryonic fission is that of Lumbricus trapezoides, in which, according to the statements of Kleinenberg (20), the embryo normally divides into two complete embryos at the gastrula-stage. In some abnormal cases, however (l. c., p. 217), a single embryo is first formed; and this gives rise to one or more embryos produced as buds on the margin of its mouth. The segmentation of the egg is described as being much less regular than in other species of Lumbricus, in which no embryonic fission takes place.

An equally striking case of the same kind had previously been described by Busch (7), in Chrysaora. In only a few cases does an egg develop into a single embryo. In the other cases, the embryo gives rise to one or two buds, apparently at the gastrula-stage; the buds becoming free larvæ, and developing fresh buds. Not only does Busch claim to have followed the whole process in an isolated individual, but he states that each time that the water in which the young larvæ were kept was changed, two thirds or so of the embryos were thrown away, and that this loss in number was compensated for, by the next day, by the gemmiparous habit of the larvæ

(l. c., p. 28). . This account is confirmed by Haeckel (14), who observed the production, in three weeks, of 60—80 buds, from ten isolated gastrulæ of Chrysaora.

The process of larval fission or gemmation is known to be even more remarkable in Aurelia (Haeckel, l. c.). Not only do the gastrulæ multiply, in some cases, by budding or by fission, but the same processes are known to occur in the Scyphostoma stage; while numerous variations are recorded in the character of the strobilation, in the multiplication of the tentacles by incomplete fission or budding, and even in the number of the highly characteristic tæniolæ and in that of the Ephyra-lobes.

The property of giving rise to fresh individuals, whether by budding or by fission, has, in this case, become a normal feature of the species; and the process takes place even at very early periods of the development, just as is the case in Crisia. The striking variability in the number of the radii of the immature stages in Aurelia may possibly be connected with something in the constitution of the egg which predisposes it to develop in an unusual way.

For since the cells which are destined to give rise to a single individual are not normally separated off until a late stage, which varies in different individuals, the existence of a tendency to vary in the number of individuals produced from an egg might also, in all probability, make itself felt in variations in a different direction. If the gastrula contains in itself the power to develop into several individuals, it is hardly surprising that it should in some cases develop an abnormal number of radii.

Similar cases of larval budding have been recorded in other Scyphomedusæ. Thus Goette (12), confirming an older observation of Sars (1841), shows that the formation of a stolon may take place (presumably in Cotylorhiza tuberculata) in the larva which has just fixed, but which is still without tentacles. Ciliated buds are also given off from the Scyphostoma of Cotylorhiza, the buds fixing' and developing a mouth after fixation.

A method of reproduction similar to the last is recorded by
Bigelow (4) in Cassiopea xamachana.

In Oceania armata, Metschnikoff (24) characterises the
process of segmentation as a regular "Blastomerenanarchie"
(p. 38). The first two blastomeres almost separate from one
another; while, in some cases, when the very slight connection
which normally exists between them becomes ruptured, the
separated blastomeres atrophy. Oceania further distin-
guishes itself, at the eight-cell stage also, from other Medusæ
investigated by Metschnikoff; the blastomeres, instead of
being arranged in an orderly manner, lying together "ganz
unregelmässig." This extraordinary irregularity (see Metsch-
nikoff's pl. i, figs. 33—35) is equally remarkable at later
stages, and ultimately gives rise to irregularly shaped masses
of cells; the embryos often assuming a quite "abenteuerliche
Gestalt," due to the fact that they multiply by divi-
sion. Those embryos which do not divide form much larger
larvæ than the others.

As a converse to this may be mentioned some most interest-
ing results arrived at by Driesch (9) and by Fiedler (10).
Driesch showed that by violent shaking of the water contain-
ing Echinus-eggs which had divided into two blastomeres,
or in other ways, the two cells could be isolated from one
another. Each segmented in the same way that it would have
followed if it had remained connected with its fellow, i. e it
developed into a half-embryo, right or left as the case might
be. The segmentation cavity, at first widely open, closed up
in course of time so as to form a blastophere, consisting (as
appeared from measuring the cells) of half the normal number
of cells, and being half the normal size. Three of these
embryos developed into complete Plutei, which differed from
normal ones only in size. In cases where the two original
blastomeres had been only partially separated, seventeen cases
were recorded in which the embryo distinctly consisted, at the
end of the first day, of two halves. In several cases each of
these embryos divided into two complete embryos, some of
which were shown to develop into small normal Plutei. In

another instance an injured two-cell embryo developed apparently normally up to the end of the blastophere stage, but finally divided into two; and in another case the injury to the two-cell stage resulted in the formation of a double monster.

In Crystallodes (Siphonophora) the remarkable amoeboid character of the superficial blastomeres suggested to Haeckel (13) that the embryo, at the end of the second day, could be compared to a colony of Amoebæ, in consequence of the great individuality of the separate blastomeres; and that, if this comparison were correct, an isolated portion of the embryo might be expected to have the power of further development. The experiments made to test this hypothesis were completely satisfactory. Embryos artificially divided at this stage developed into normal individuals of a smaller size than usual. The cut surface became concave, the edges ultimately joining, so that the embryo again became spherical, and then proceeded to develop in its normal manner.

It is hardly possible to overlook the fact that, in some at least of the above quoted cases, embryonic fission is specially connected with deviation from the normal type of segmentation of the egg. This is most clearly seen in the case of Oceania, where a superficial glance at Metschnikoff's figures is sufficient to convince one of the extraordinarily abnormal character of the segmentation. The same fact is, however, to some extent true of Lumbricus trapezoides and of Crystallodes, where Kleinenberg and Haeckel respectively call attention to remarkable features in the segmentation.

The segmentation of the egg of Crisia obviously belongs to an unusual type, and, as has already been pointed out, it finds its closest parallel in Salpa, an animal which is remarkable for the great extent to which asexual reproduction is carried out.

Doliolum, whose life-history agrees with that of Salpa in including two remarkably different generations, offers a further analogy to Crisia in the character of its asexual reproduction. The stolon of the asexual generation segments off, according to

the description of Uljanin (35), a series of buds in which
there is a very small amount of differentiation. These " Ur-
knospen " consist of a layer of ectoderm surrounding a mass of
embryonic cells which are but slightly differentiated (l. c., pl.
x, fig. 3). These buds divide up into numerous similarly-
constituted buds, so that the sexual individual of Doliolum
takes its origin from a group of cells which is very similar to
the young " secondary embryos " of Crisia.

The same method of reproduction characterises the remark-
able Dolchinia, recently described by Korotneff (22). This
animal is closely allied to Doliolum, if, indeed, it should not
be placed in that genus. The only phase in its life-history
which is so far known is a gelatinous axis, bearing very nume-
rous Doliolum-like zooids, and which probably corresponds
to the dorsal process of Doliolum. The axis bears numerous
buds, wandering about on its surface by means of pseudo-
podia. The buds have probably been derived from the seg-
mentation of the ventral stolon of an asexual form. They
increase in number by division. Should one of the daughter-
buds fix itself on the base of a young zooid, it becomes a
bean-shaped body, which gives rise to a large number (as
many as forty) of new buds. The young buds, at the stage at
which they become free, consist of a solid mass of cells in
which a very small amount of differentiation has taken place.

The formation of the secondary buds, as shown in Korot-
neff's pl. xiii, figs. 14, 15, has thus a striking resemblance to
the mode of development of the secondary embryos in Crisia;
neglecting the not unimportant difference that in the former
case the budding organ is itself a bud, and in the latter case
an embryo.

A similar process probably takes place in Anchinia (21);
and Uljanin (l. c., pp. 106—117) brings forward evidence to
show that the same is true of some of the compound Asci-
dians. The larva of Distaplia magnilarva, for instance,
gives rise to structures comparable with the " Urknospen " of
Doliolum. Uljanin comes to the conclusion that the bud-
ding of adult Tunicates is derivable from a division of " very

young developmental stages." A similar suggestion with regard to the origin of alternation of generations among the Hydromedusæ has also been elaborated by Brooks (6), who supposes that the hydroid stage has been evolved by the acquirement of the power of budding by the fixed larval stage.

A slight modification of the "primary embryo" of Crisia would suffice to make it necessary to consider the life-history of that animal as a case of alternation of generations. But since, as I believe, the budding structure consists of a mass of embryonic cells, which ultimately becomes completely converted into "secondary embryos," leaving nothing behind, I have preferred not to describe it as a separate generation.

Enough has been said to show that in the Tunicata at least, and to a less extent in the Cœlenterata,[1] there are remarkable cases of the formation of buds from slightly differentiated masses of cells. These two groups, with the Polyzoa, are certainly the groups of animals in which budding in the adult condition is a more normal event than in other groups of animals.

It may thus be asserted that in the Polyzoa, the Tunicata, and the Cœlenterata the asexual reproduction of certain forms takes place at a stage before the individual which is reproducing asexually has had time to undergo more than the earliest steps in its development. A similar precocious formation of fresh individuals is well known in the reproduction of Trematoda.[2]

The investigations of Driesch (9) and of Haeckel (13) have shown that blastomeres which have been artificially separated from the embryo are able, in some cases, to give rise to complete larvæ. The question suggests itself: Has the gemmi-

[1] The case of Cunina, as described by Uljanin, Schulze, Metschnikoff, and Brooks, and more recently by O. Maas ('Zoolog. Jahrbücher,' "Abth. f. Anat. u. Ontog.," Bd. v, Heft 2, 1892), is another remarkable instance of the same kind.

[2] Compare particularly the remarkable account given by Heckert (18) of the life-history of Distoma macrostomum, and particularly the statements referring to its remarkable branched sporocyst, known as Leucochloridium paradoxum.

parous method of reproduction in the adults of the above-mentioned groups been preceded by larval fission, possibly induced by the separation from the embryo of individualised blastomeres or groups of blastomeres, or is the embryonic fission the result of the precocious acquirement of the budding habit which characterises the adult? Now in the Polyzoa, embryonic fission is by no means a common phenomenon, although the adults of all known Polyzoa possess the power of budding; and although it is probable that the method of reproduction above described in Crisia will be found to be characteristic of all Cyclostomes. I have no sufficient evidence on this point at present, but it may be pointed out that the ovicells of Cyclostomatous Polyzoa invariably (so far as I know) contain a large number of embryos. My own observations enable me to state further that the general structure of the ovicell in Idmonea serpens and in Diastopora patina agrees with that in Crisia; and I have little doubt that I shall be able to show that embryonic fission is characteristic of Cyclostomes in general. The development of the Phylactolæmata possibly offers some analogies to this process. The structure of the larva is somewhat similar to that of Cyclostomes, and the early development, according to the account given by Jullien (19), is not unlike that of Crisia. Braem (5) has also given an incomplete account of the development of Plumatella, which suggests further resemblances to the Cyclostomata. The two layers which form the wall of the embryo, and which are considered by Braem to represent ectoderm and body-cavity epithelium respectively,[1] are obviously comparable with the two layers shown in Pl. III, figs. 22 and 23, of Crisia. The manner in which (in Plumatella) a rudimentary bud encloses the egg, forming the "oœcium," is again strikingly suggestive of Crisia.[2] The first stage in which the

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[1] The same conclusion is arrived at by Davenport (8A), whose valuable paper should be consulted for a comparison of the larva of Phylactolæmata with that of Gymnolæmata.

[2] Compare in particular the woodcut given by Braem in his explanation to fig. 171.

egg is completely enclosed is shown in Braem's pl. xv, fig. 171, while in fig. 172 the " ooecium " has differentiated off a distal portion which may be the exact equivalent of the " tentacle-sheath " shown in my own fig. 3 for Crisia. The tendency to precocious fission shows itself in Phylactolæmata, however, in the precocious formation of a considerable number of polypides, particularly in Cristatella;—a process which is of course very different from the embryonic fission of Crisia.

The ovicells of the Cheilostomata are probably not homologous with those of Cyclostomata. They are probably not to be regarded as modified zoœcia, since the ovicell is an appendage of a fertile zoœcium, and ordinarily contains a single embryo.

Similarly in the other groups which have been mentioned precocious fission is not characteristic of the whole group, but occurs sporadically;—in Cœlenterata, in Oceania, Cunina, &c.; in Trematoda, in the Distomeæ; and in Tunicata in the Thaliacea, and in some Synascidians.

Although I must regard the question as a very open one, the conclusion which appears to me to be suggested by the above facts is that one is not justified in assuming that the budding of the Polyzoa, for instance, commenced with the acquirement of a habit of embryonic fission like that found in Crisia, but that the embryonic fission may be the consequence of the previously acquired power of adult budding. It may be pointed out that the embryonic fission of Crisia gives rise to numerous larvæ, each of which may form the starting-point of a new colony. In the case of adult Polyzoa, the result of budding is merely to increase the number of individuals in a colony, with the exception of Loxosoma (in which the bud normally becomes free) and of certain dendritic forms of colony, in which the decay of the proximal part of the colony leads to the separation as distinct colonies of what were at first merely branches, or of cases like that of Crisia itself, where new colonies are formed by the upgrowth of new stems from a creeping rootlet, which acts as a stolon for the production of

new colonies.[1] It should be further noted that the production
of new polypides in old zooecia is one of the most characteristic
ways in which the property of budding manifests itself in
Ectoprocta, and that this process is most easily interpreted as
a process of regeneration of lost parts.

The provisional conclusion may therefore be stated as
follows :—That the process of embryonic fission, which may
appear abnormally in certain individuals in so many groups of
animals which do not multiply by fission, has in Crisia become
a normal phenomenon of the development ; and that this pro-
cess is correlated with the tendency which is so strongly
marked in the Polyzoa to produce buds in the adult condition.

Giard (11) has recently published a note on what he terms
" poecilogonie," i. e. the phenomenon exhibited by certain ani-
mals of developing in a more or less " condensed " manner, in
correlation with the amount of nutritive reserves in the egg,
or with the conditions under which the parent is living. As
examples of this process are mentioned, inter alia, the follow-
ing cases :—In Leptoclinum lacazii, Gd., the same colony
may produce two sorts of eggs ; of these, one is poor in yolk,
and gives rise to small larvæ, whose tail is absorbed early, and
which do not begin to bud even on the third day. The other
kind is rich in yolk, and produces larvæ which are still free-
swimming on the fourth day, and which then already contain
a colony of three individuals. Ophiothrix fragilis, Müll.,
lays eggs which develop, according to the conditions, either
into perfect or into imperfect Plutei, or into embryos incapable
of swimming, and which develop directly. The remarkable
variations in the development of Aurelia aurita and of
Palæmonetes varians are also included in this category ; in
the latter form the size and number of the eggs, as well as the
rapidity of the metamorphoses, varying according as the animal
lives in the brackish waters of the North or in the fresh-water
lakes of the South.

Giard's observations suggest that the acquirement of em-

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[1] The statoblasts of the Phylactolæmata are indeed a further exception,
since each of these bodies is able to give rise to a new colony.

bryonic fission in Cyclostomes may have been connected with the presence of the nutritive conditions which are suited to induce the precocious formation of buds. Nothing can be more striking than the obvious continuity of protoplasm between the several units of the colony in a decalcified branch of C r i s i a. In the individuals which are modified as ovicells the protoplasmic network is particularly well developed. The embryo is thus surrounded by a rich nutritive material; and just as the presence of a nutritive placenta in a Placental Mammal has resulted in the diminution of the size of the ovum, and in various abnormalities in its early segmentation, so in C r i s i a the size of the egg is reduced to a minimum, the whole of the nutritive substance being retained in the parental tissues and handed on to the egg or embryos as required, while the segmentation is entirely abnormal. Further, while the Mammalian embryo becomes easily comparable with that of any other Vertebrate embryo after a certain number of the early stages have been passed through, so the C r i s i a larva becomes, to some extent at least, comparable with the free larva of any other Polyzoon, although with this difference from other Polyzoa, viz. that the primary embryo has given rise to numerous larvæ, a process comparable with the artificial production of a complete embryo from a single blastomere of the two cell stage in the experiments of Driesch (9) and of Fiedler (10).

Attention has already been called to the similarity between the early stages of the development in C r i s i a and those in S a l p a. The latter is another example of the modification of the first processes in the development, associated with the presence of special maternal nutritive arrangements. The embryo of S a l p a develops, as is well known, in close connection with a kind of placenta; and its early stages are, compared with those of most other animals, highly abnormal. The formation of buds from the individual developed from the egg does not take place at once, as in C r i s i a, but is deferred until the animal is mature, when buds are produced in very large numbers from the stolon.

Similarly the egg of Pyrosoma, like that of Salpa, makes its appearance in the same precocious manner as that of Crisia, being formed very early from the so-called "genital string" (Salensky, 29). The early development, which is modified by the presence of yolk, takes place in the interior of the old colony, and is very abnormal, the blastomeres being for a time completely separated from one another (Salensky, p. 443). The result of the development is the formation of the well-known "Cyathozooid," with its colony of four "Ascidiozooids," the formation of which is compared by Salensky (30, p. 92) with the embryonic fission of Lumbricus trapezoides. The formation of a stolon (represented by the chain of four Ascidiozooids) in the Pyrosoma-embryo is further regarded as the precocious acquirement by the embryo of the power of budding already possessed by the Synascidians.

Peripatus[1] is well known to be viviparous, and the extraordinary character of the segmentation of its ovum may have some relation to the presence of external sources of nutriment.

The cases already quoted may be taken as showing that some of the abnormalities in the development of Crisia may be due to the nutritive conditions in which the development takes place. Just as the presence of food-yolk within the egg modifies the character of the segmentation and of the formation of the layers, so the presence of copious stores of nutrient material in the maternal tissues outside the egg may also affect the early developmental processes. Thus the large number of relatively large larvæ which develop from the minute egg of a Crisia could not be produced if the egg were not supplied with nutriment from outside itself. While some of the irregularity in the segmentation of the egg may be due to this cause, the extreme independence of the blastomeres at an early stage may be connected with the acquirement by the embryo of a habit of forming buds in the embryonic condition.

[1] See Sedgwick, No. 31.

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It hardly falls within the province of this paper to discuss the details of the normal budding in Polyzoa. Both Braem (5) and Davenport (8A) have shown that polypide-buds in general are derived from a mass of "embryonic" tissue, handed down from the beginning of the formation of the colony, some part of this tissue being left over for the production of fresh buds on each occasion when a polypide-bud is formed. Braem's account of the formation of the statoblasts in Phylactolæmata more nearly resembles the development of the "secondary embryos" in Crisia than any other process as yet described in Polyzoa. The funiculus is, indeed, not an embryo; but the young statoblasts are formed from it in much the same way as that in which the larvæ are developed from the "primary embryo" in Crisia. The funiculus consists of a core of ectoderm surrounded by a sheath of mesoderm (both kinds of cells having an "embryonic" character). The statoblasts are formed by a process which is to all intents and purposes a transverse segmentation of the funiculus.

EXPLANATION OF PLATES I, II, & III,

Illustrating Mr. Sidney F. Harmer's paper "On the Occurrence of Embryonic Fission in Cyclostomatous Polyzoa."

PLATE I.

FIG. 1.—Crisia eburnea. Median longitudinal section through a young ovicell, showing the egg, which is already partially surrounded by the polypide-bud (Zeiss, DD).

FIG. 2.—C. ramosa. Part of a similar section at a more advanced age, showing the complete inclusion of the ovum (Zeiss, DD).

FIG. 3.—C. ramosa. Similar section at an older stage. The polypide-bud has become the "follicle." The tentacle-sheath and the aperture are well developed. Ovicell at the "funnel-stage" (Zeiss, DD).

Fig. 4.—C. eburnea. Spermatozoa. To the right, three mature spermatozoa, drawn in the living condition (Zeiss, F); to the left, three stages in the development of the spermatozoa, treated with osmic acid and picro-carmine (Zeiss, F); in the middle, four immature groups consisting of four spermatozoa each, killed with osmic vapour (Zeiss, $\frac{1}{18}$ immersion, 4 oc.).

Figs. 5—7.—C. ramosa (Zeiss, DD).

    Fig. 5. (Combined from several sections of the same ovicell.) The egg has divided into three blastomeres; the valve is developing, and the distal end of the tentacle-sheath has become thickened.

    Fig. 6. Proximal end of a longitudinal section (more advanced). The embryo consists of a compact rounded mass lying in a large follicle, which projects freely into the tentacle-sheath.

    Fig. 7. A similar preparation at a stage when the vacuolation of the follicle is commencing.

PLATE II.

Fig. 8.—Crisia eburnea. Ovicell at a stage corresponding to Fig. 6 in C. ramosa. The embryo is larger and the follicle is much smaller than in that species (Zeiss, DD).

Figs. 9—14.—C. ramosa (Zeiss, D D).

    Fig. 9. The vacuolation of the follicle is nearly complete. The tubular aperture is formed, and the structures connected with its base are well developed.

    Fig. 10. Invagination (?) in a "primary embryo," at about the same stage as Fig. 9.

    Fig. 11. Considerably later stage. The follicle has become a dense protoplasmic reticulum, containing the massive "primary embryo," now transformed into a budding organ, which is giving rise to numerous secondary embryos, three of which are seen lying freely in the reticulum. At the upper end a giant-cell, derived from the thickened distal end of the tentacle-sheath (cf. Figs. 5, 13 and 9).

    Figs. 12—14. Illustrating the development of the aperture of the ovicell. In Fig. 12, the primary aperture still remains open, the distal end of the tentacle-sheath being thickened. In Fig. 13, the tubular aperture of the adult ovicell is developing; it contains the remains of the primary aperture. The thickening of the distal end of the tentacle-sheath has increased in size, and the valve is well developed. In Fig. 14, the tubular aperture is almost complete. The thickening of the tentacle-sheath still extends into its base. At its distal end a depression occurs, which is possibly the remains of the primary aperture. The tube ends in a cap prolonged into a narrow tube, of unknown significance.

PLATE III.

FIG. 15.—Crisia eburnea. A young internode decalcified, with a developing ovicell. For explanation of the letters (A, B, and c) see p. 5 (Zeiss, A).

FIGS. 16—23.—C. ramosa.

Fig. 16. The aperture of the same ovicell from which Fig. 6 was taken. The origin of the giant-cells from the thickened distal end of the tentacle-sheath is shown (Zeiss, F).

Fig. 17. Longitudinal section of an ovicell which is filled with secondary embryos. To the left, the primary embryo (Zeiss, A).

Fig. 18. Protoplasmic reticulum with giant-cells, from an ovicell at about the stage of Fig. 11 (Zeiss, F).

Figs. 19—21. Development of ovicell (Zeiss, A). The ovicell has in each case been numbered 4, in order to admit of ready comparison between the three stages.

Fig. 22. Young secondary embryo, in longitudinal section (Zeiss, F).

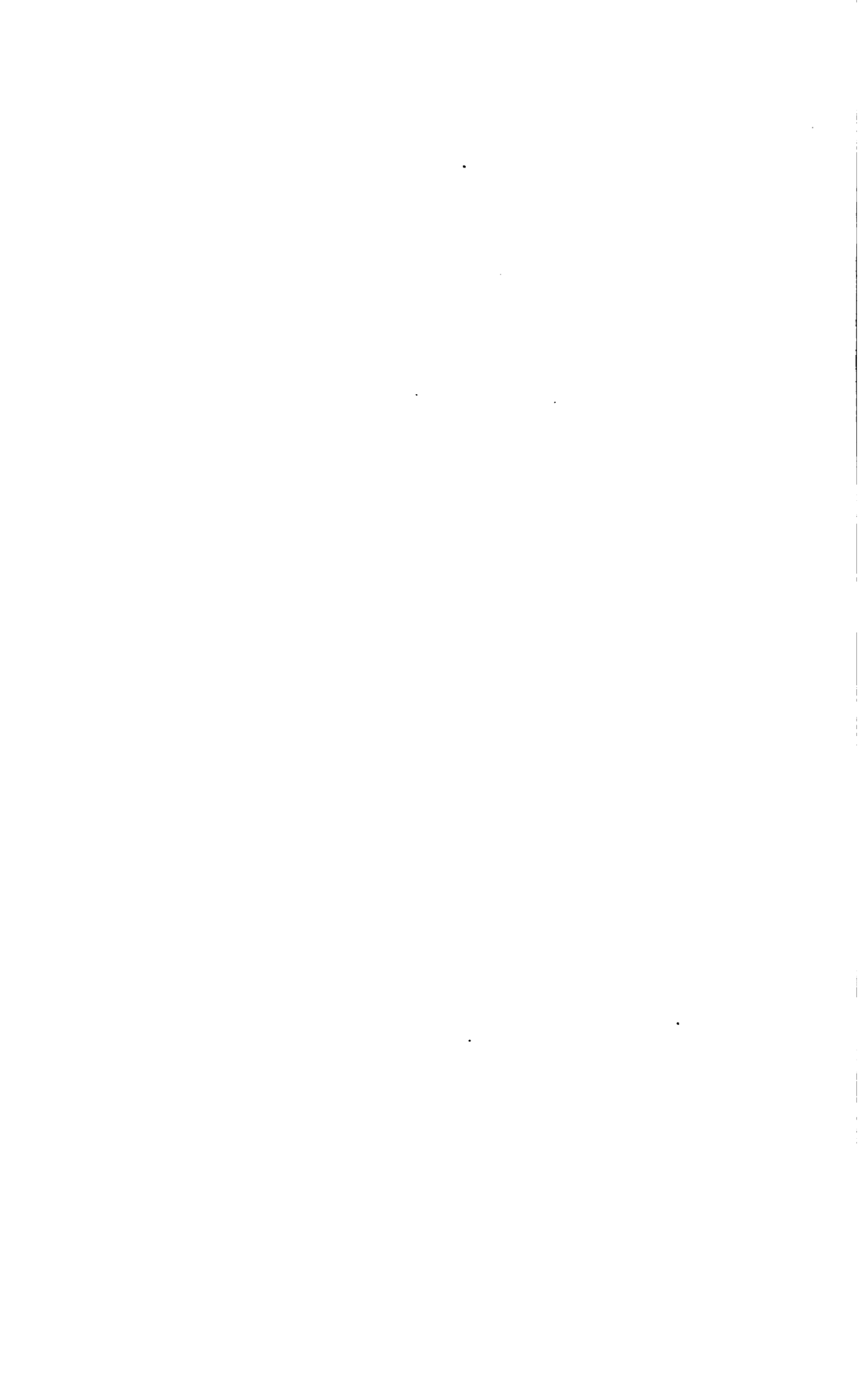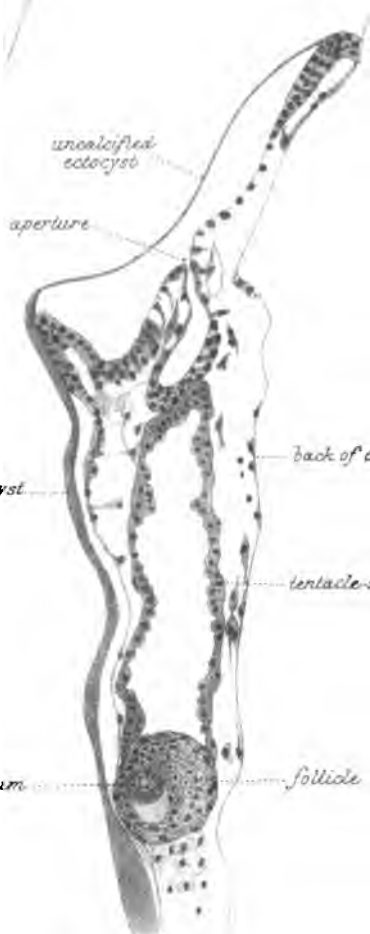Fig. 23. Older embryo, in longitudinal section (Zeiss, F).

Fig. 1.

Fig. 2.

Fig. 5.

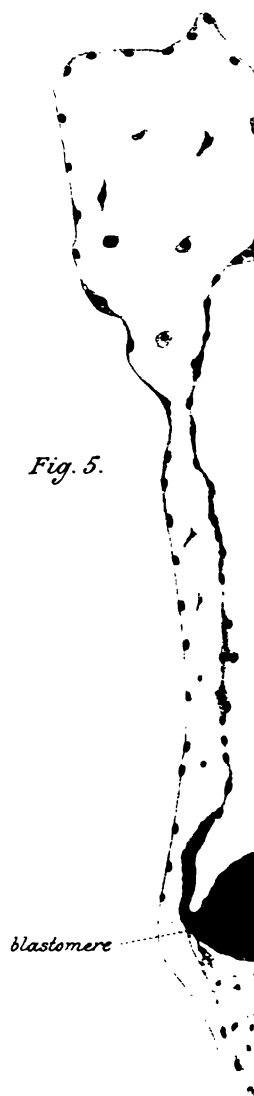tentacle sheath

ovum

uncalcified
ectocyst

aperture

Fig. 3.

back of ovicell

calcified ectocyst

tentacle sheath

ovum

follicle

blastomere

S F Harmer del

$\mathcal{V}$. 4.

Fig. 6.

embryo

follicle

tentacle-sheath

aperture

valve

tentacle-sheath

back of ovicell

follicle

Fig. 7.

stomachs of
polypides

embryo

tentacle-sheath

follicle

Fig. 8.

Fig. 9.

beginning of tubular aperture

calcified ectocyst

tubular aperture

valve

tentacle-sheath

giant-cells

back of ovicell

tentacle-sheath

follicle

embryo

S. F. Harmer del.

Fig. 10.

Fig. 12.

Fig. 11.

---valve

Fig. 13.

giant cell

secondary
embryos

valve

tentacle-sheath

vacuolated
follicle

Fig. 14.

embryo

primary
embryo

follicle

acuolated
follicle

tentacle-sheath

Fig. 15.

Fig. 16

Fig.

ovicell

C

B

beginning
of branch

A

tubular aperture

valve

aperture

Fig. 17.

valve

young embryos

primary embryo

zoœcia

Fig. 18.

S. F. Harmer del.

9.

Fig. 20.

6   7

4

3

2

1

Fig. 21.

8   7

6

4   5

3

2

Fig. 22.

inner layer

sucker

Fig. 23.

lining of future
mantle · cavity

inner layer

sucker

The Early Stages in the Development of Distichopora violacea, with a Short Essay on the Fragmentation of the Nucleus.

By

Sydney J. Hickson, M.A. Cantab. et Oxon., D.Sc.Lond.,
University Lecturer on the Morphology of Invertebrates; Fellow of
Downing College, Cambridge.

With Plate IV.

THE material upon which I have made my investigations was in part collected by me in N. Celebes, and in part by Professor A. C. Haddon in Torres Straits. Some of the specimens were treated with strong alcohol alone, others with corrosive sublimate followed by alcohol. For decalcification I have entirely used nitric acid.

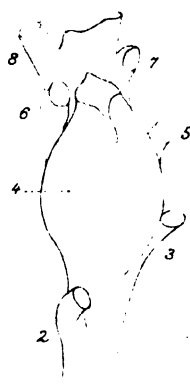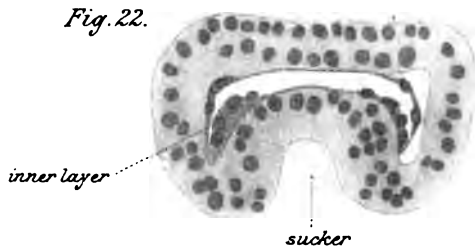I have tried a great many different stains and combinations of stains. Borax carmine, Biondi's fluid, methyl green, and hæmatoxylin all give fairly good results; but I find that the best treatment is to place the sections, when fastened to the slide, in a strong solution of eosin in 90 per cent. spirit for an hour, then to wash in 90 per cent. spirit and stain in weak hæmatoxylin for twenty minutes. This treatment gives a beautiful double stain which shows the nuclei and the chromatin granules better than I have seen them in any preparations treated with carmine.

My researches were entirely carried on in the morphological laboratory at Cambridge.

I. The Early Stages in the Development of Distichopora.

The ovum of Distichopora, like that of Allopora and other Stylasterids, is provided with a large amount of yolk, and lies in a cup-shaped trophodisc.

In young immature ova the germinal vesicle is situated in the middle of the egg, is spherical in shape, is provided with a well-defined membrana limitans, a germinal spot, and a fine network of protoplasmic fibrils with thickened nodes (Pl. IV, fig. 1).

When examined with a high power the germinal spot may be seen to contain a few clear vacuoles (fig. 2).

In some ova with a full complement of yolk-spheres the germinal vesicle is irregular in shape, and provided with processes resembling the pseudopodia of amœba. The outlines of these processes are usually difficult to observe, the membrana limitans being apparently wanting, and the intra-nuclear and extra-nuclear protoplasm perfectly continuous (fig. 3).

In these cases there may be seen a few large rod-shaped granules (the chromosomes), which stain deeply with carmine and other stains.

These amœboid germinal vesicles are without doubt passing from the centre of the ovum towards the periphery. In those that are near the periphery the chromosomes are more numerous and very much smaller than they are in those nearer the centre of the ovum. In one case I have observed these bodies arranged in a row parallel to the surface of the ovum, and dividing the nucleus into two unequal halves (fig. 5).

When and in what manner the polar bodies are formed I cannot say, but it is probable that in some cases the nuclei of the polar bodies are formed before the germinal vesicle reaches the periphery, and are absorbed in the substance of the ovum. The germinal vesicle finally reaches the periphery of the ovum, and when it is in that position the fertilisation most probably occurs.

It is clear that the germinal vesicle must remain at the

periphery for a very considerable time, for of the numerous unfertilised ova that I have examined a large majority have their germinal vesicles in that position.

In the next stage the membrana limitans of the inner half of the vesicle disappears, the network and the germinal spot break down into numerous very minute scattered granules (fig. 7).

Then the membrana limitans entirely disappears, and lastly, the substance of the vesicle, or, as it should now be called, the oosperm nucleus, becomes scattered through the substance of the ovum.

Fig. 8 is a careful drawing of a stage in which the membrana limitans has just disappeared, and I have three or four complete series of sections through ova in which no trace of nuclear structure can be found nor any area, such as that shown in this figure, which represents the vanished nucleus.

As these two stages are of the greatest importance in the consideration of what follows, it is necessary to say that notwithstanding very careful search with high powers, no trace of karyokinetic figures could be observed.

The ova of these stages are not sufficiently numerous, nor are the methods of preservation sufficiently perfect to enable one to assert that such figures do not occur. Corrosive sublimate followed by alcohol, although giving excellent general histological results, does not always bring out the full details of nuclear division; and it will be necessary to confirm these purely negative results as regards karyokinesis by observations made upon specimens preserved in Flemming's solution and other reagents before any general statements regarding fragmentation of the oosperm nucleus of Distichopora can be accepted.

Nevertheless it is my belief that we have here an instance of nuclear fragmentation, for reasons which I propose to discuss in the third section of this paper.

In the next stage that I have observed, a few small islands of protoplasm may be seen in the yolk (fig. 9), and the examination of broken sections, in which part of the yolk has

been washed away, shows that these islands are connected together by a very coarse mesh-work of fine protoplasmic strands.

In a later stage the islands are seen to be more numerous, and the protoplasmic mesh-work somewhat finer. A complete nucleus may be seen in some of these islands, but in others all that can be made out are a few deeply staining granules (figs. 10 and 12).

In a later stage the nuclei have increased in number in the midst of the yolk, and a few make their appearance in the protoplasmic sheath that surrounds the ovum.

In these last three stages I have described a process which can only be compared with the so-called free nuclear formation in early insect embryos. Nuclei make their appearance in places which were previously apparently devoid of any nucleus or nuclear structure. Moreover nuclei of various sizes and shapes may be seen in the embryo at the same time.

It is not reasonable, however, to assume on the insufficient evidence before us that "free nuclear formation" does actually occur. It seems to me to be much more probable that minute fragments of nuclear substance scattered through the protoplasmic mesh-work collect together in places, and form by their fusion true recognisable nuclei. In other words, the process we have under observation is rather one of "nuclear regeneration" than one of "free nuclear formation."

I have often noticed in ova of these stages an aggregation of the yolk into spherical, polygonal, or irregular lumps, suggesting that the egg has undergone some form of complete segmentation (fig. 13). This is not a true process of segmentation, however, since the distribution of the nuclei in the spaces between the aggregations and not in their centres shows that it affects the yolk only. It is remarkably similar in appearance to the so-called yolk segmentation of Arthropods, the appearance of the embryo at this stage being very much like that of such a form as Peripatus novæ-zealandiæ, as described by Miss Sheldon (53). This segmentation of the yolk seems to be only temporary, for in embryos in which the

ectoderm has commenced to be differentiated it cannot be observed. In later stages of the development the ectoderm is gradually formed. Nuclei appear in the peripheral sheath of protoplasm, and the protoplasm accumulates in the form of cellular blocks around each nucleus, as in Allopora.

I have carefully examined the endoderm in these stages in the hope of finding out the manner in which the nuclei divide, and although I have found a few dumb-bell-shaped forms, and no satisfactory evidence of karyokinesis, I do not feel justified in asserting that the nuclei always divide amitotically.

As far as the ectoderm is concerned, I can assert most positively that indirect nuclear division does occur.

Numerous dumb-bell-shaped nuclei and nuclei connected together in pairs may be seen in the developing ectoderm, and in these faint achromatic lines may be seen connecting the chromatin rodlets. The nuclei are too small to enable me to make out all the details of the process, but there can be no doubt that there is a true process of karyokinesis in the divisions of these nuclei (fig. 18, *a, b, c, d,* and *e*). I have not been able to decipher anything like the "spheres of attraction."

One very remarkable and important point in the development of all the Hydrocorallinæ, so far as they have at present been investigated, is the fact that there is no segmentation of the ovum, either complete or partial, nor is there any formation of cells with a definite outline until a very late stage.

At the time when (in Allopora and Distichopora) there are ten or fifteen nuclei, the young embryo is a simple multinucleated plasmodium, loaded with yolk. In the later stages the nuclei have increased in numbers, and a certain number of them are arranged in a row at the periphery of the embryo.

The yolk in the immediate neighbourhood of these peripheral nuclei disappears, probably by absorption, and thus they are situated in a clear peripheral sheath or envelope of protoplasm. In a later stage this peripheral sheath of nuclei breaks up into blocks, each block containing one nucleus, and thus the ectoderm is formed.
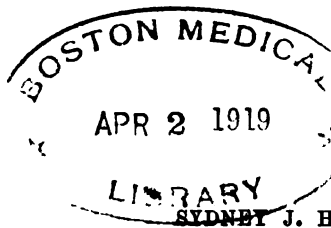
The ectoderm is, then, a differentiation of the periphery of a multinucleated plasmodium.

What becomes of the inner part of the plasmodium?

We have no answer to this question so far as the Hydrocorallines are concerned; but, judging from the other Cœlenterates, there can be little doubt, I think, that it becomes the endoderm.

In the development of Aglaophenia (Tichomiroff, 55) we find a stage that is almost precisely similar to the solid planula of Distichopora and Allopora, and in a later stage this central yolk-laden plasmodium breaks up into blocks, which become the endoderm-cells of the adult.

The difficulty that we have now to face is, how can these facts concerning the origin of the germ layers be brought into line with those of other Cœlenterates?

We find in the Stylasteridæ no segmentation, no process of invagination to form the endoderm, and no process that can be compared with ordinary primary delamination; but still it is probable that this method of the formation of the germ layers, if it is not itself the primitive one, has been derived from those of other Cœlenterates, and I shall endeavour to show in the next section how the transition has taken place.

II. On the Formation of the Germinal Layers in the Cœlenterata.

During the last ten years our knowledge of the early stages of the development of the Cœlenterata has very considerably widened, but still we seem to be no nearer to the solution of many interesting phylogenetic questions than we were before. The various theories that have been put forward, based upon the study of a few forms, have in no instance received the unqualified approval of the principal authorities on the group, and we find ourselves in a maze of conflicting theories, none of which seem to conform entirely to our knowledge of facts.

This unfortunate state of affairs is due to the fact that in the group of the Cœlenterata we find many very different types of

development, and no one of them seems to be particularly predominant.

The development of a gastrula by invagination probably occurs only in the group of Scyphomedusæ.

The formation of a planula by delamination (i. e. the primary delamination of Metschnikoff) occurs only in the group of the Geryonidæ.

The formation of a sterrula by secondary delamination occurs in most of the Anthozoa (McMurrich) and in many of the Hydroids.

The formation of a sterrula by hypotropic invagination occurs in many Sertularidæ and Campanularidæ.

The formation of a planula or sterrula by polypolar immigration of cells into a hollow blastula occurs in a few forms.

Lastly, the formation of a multinucleated plasmodium without segmentation, which is followed by the differentiation of epiblast-cells at the periphery of a solid plasmodium (the endoderm), occurs in the Hydrocorallinæ and in some Alcyonarians.

Between these various types of development many intermediate forms have been found, so that we have as it were a complete series of developmental histories, with the typical invaginate gastrula at one end and the multinucleated plasmodium at the other.

We may represent this series by the following plan :

A. Gastrula formed by invagination.   Large segmentation cavity.

Examples: Cotylorhiza (Claus, 8), Pelagia noctiluca, and Nausithoë (Metschnikoff, 42).

a. Intermediate forms between type *A* and *B* are found in Aurelia flavidula (Smith, 52), in which the clump of cells that are invaginated is at first solid, and in Cyanæa capillata (McMurrich, 41), in which this clump of cells remains solid longer than in A. flavidula.

B. A solid planula (sterrula) formed by hypotropous immigration of cells into a large segmentation cavity.

Examples: Clytia, Tiara, Rathkea, Obelia, Tima, Æquorea (Metschnikoff, 42), and Cyanæa arctica (McMurrich, 41).

b. Intermediate forms, in which the migration takes place mainly at the hind end, occur in Mitrocoma (Metschnikoff, 42).

C. A sterrula is formed by polypolar immigration of cells into a large segmentation cavity, these cells being formed by the radial fission of the cells of the cœloblastula.

Example: Æginopsis (Metschnikoff, 42).

c. Intermediate form, in which the cells that immigrate are formed partly by radial and partly by tangential division.

Example: Hydra (Brauer, 5).

D. A planula is formed by primary delamination, the endoderm-cells formed by tangential division only. The segmentation cavity is large.

Example: Geryonia (Metschnikoff, 42).

d. Numerous intermediate forms in which the segmentation cavity is small.

Examples: Tubularia (Brauer, 5a), Bougainvillea (Gerd, 14).

E. A sterrula is formed by precocious delamination (secondary delamination of Metschnikoff). No segmentation cavity formed.

Examples: Aglaura (Metschnikoff, 42), Rhopalonema (Metschnikoff), Eudendrium and Sertularella (Tichomiroff, 55).

e. Intermediate forms in which the segmentation is at first incomplete.

Examples: Renilla (Wilson, 63), Gorgonia (von Koch, 36), and probably other Alcyonarians.

F. A multinucleated plasmodium is formed. There is no segmentation and no segmentation cavity.

Examples: Algaophenia (Tichomiroff, 55), Mille-

pora (Hickson, 17), and the Stylasteridæ (Hickson,
18 and 19).

It is not my purpose to discuss fully the various views that
have been put forward concerning the origin of the Metazoa
from the Protozoa. The gastrula theory, the planula theory,
the plakula theory, and the phagocytella theory have each
received in their turn the consideration of naturalists, and
nothing would be gained were an attempt made in these pages
to reopen the discussions that they gave rise to.

But I cannot pass on without expressing my opinion that
the developmental history of the Hydrocorallinæ lends some
support to the so-called " plasmodium " theory. Many years
ago, Jehring (27) and Saville Kent (32) put forward the view
that the Metazoa are derived from a multinucleated Protozoan
like Opalina. Sedgwick (57) has supported this view, as a
result of his important work on the development of Peripatus,
and considers that the ancestral Metazoan was probably of
" the nature of a multinucleated Infusorian, with a mouth
leading into a central vacuolated mass of protoplasm."

In discussing Saville Kent's views Metschnikoff (42) says
that there is no evidence of the formation of such a multi-
nucleated cell in the lowest Metazoa.

Now I have already pointed out that in the earliest stages
of the Stylasteridæ and of Millepora the embryo is nothing
more nor less than a multinucleated cell; that is to say, it is a
single undivided mass of protoplasm, containing numerous
nuclei. It might be urged that it is a syncytium, a number
of cells fused together; but there is no more evidence for
such a view than for the view that it is a single multinucleated
cell.

Similarly it may be urged that Tubularia (Brauer, 5 a),
Aglaophenia (Tichomiroff, 55), Alcyonium (Kowalewsky, 37),
Gorgonia (von Koch, 36), and Renilla (Wilson, 63) all pass
through a stage in their development in which the embryo is
simply a multinucleated cell.

The fact that such a condition as this occurs in many
different groups of the animal kingdom widely separated from

one other also lends support to the view that it may have some important phylogenetic significance.

Instances of the occurrence of an unsegmented multinucleated plasmodium are found not only in the Cœlenterata above mentioned, but in Peripatus, Myriapods, Spiders (Kishinouye, 34, and Morin, 44), Insects, Crustacea, Elasmobranchs, and probably many other forms with large eggs.

It might be urged as an argument against the plasmodium theory that the multinucleated plasmodium occurs principally in the development of those forms whose ova contain a large amount of food-yolk, that the segmentation is modified by the presence of this yolk, and that consequently the phylogeny is obscured.

But it does seem to me that in the ovum that is perfectly clear and homogeneous we have a cell that is any nearer to the ancestral Protozoan than the ovum that contains a moderate amount of yolk.

It is almost certain that the ancestral Protozoan normally contained some food-vacuoles, and it is quite as probable as not that it had some contractile or simple water-vacuoles for floatation purposes as well.

It is quite as reasonable to suppose that the Metazoa are derived from an Actinosphærium-like ancestor with vacuoles in the outer regions as well as in the inner mass, as it is to derive the Metazoa from a " multinucleated Infusorian with a mouth leading into a central vacuolated mass of protoplasm."

If this is the case, then we can no longer consider the yolk-bearing eggs to be secondarily modified, and the small transparent eggs to be the primitive types from which all the others are derived; but we may expect to find in the development of eggs with a moderate amount of yolk just as much or even more evidence of ancestral history as in eggs that are practically yolkless.

It must not be forgotten, moreover, that the occurrence of a multinucleated plasmodium is not confined to those cases in which the ovum contains a large amount of yolk.

In the ovum of Millepora there is no yolk, and yet the

oosperm nucleus fragments without any segmentation occurring, giving rise to a simple multinucleated plasmodium.

The eggs of Aphis (Will, 62) and some other insects contain very little yolk, and do not segment until a large number of nuclei are formed.

The segmentation of the ovum, then, and the subsequent formation of a morula mass of cells, are phenomena not entirely dependent upon the absence of yolk. Many, comparatively speaking, large eggs, such as that of Rana, segment, whilst others, such as that of Alcyonium, do not.

We cannot, consequently, assert that when an ovum segments it is simply repeating an ancestral phase, and that when it does not segment it is prevented from doing so by the physical obstruction of the yolk.

The reverse of this is more probably true. The recent brilliant researches of Driesch (9) prove that the segmentation of the ovum is due to physical or mechanical laws, and we cannot or should not derive any phylogenetic conclusion from the phenomena of segmentation.

We may even go further than this, and say that the developing ovum would not segment, but would naturally pass through the stage of a multinucleated plasmodium, were it not for the action of certain purely mechanical forces, with which we are not at present fully acquainted. When these forces cannot act upon the egg, or are in some way counteracted, the ovum does not segment, whether it is laden with yolk (Stylasteridæ, many Insects, Elasmobranchs, &c.) or not (Millepora).

III.—On the Fragmentation of the Oosperm Nucleus.

It is the belief of many eminent histologists that any process of division of the nucleus other than that by karyokinesis or mitotis is a sign of the degeneration of the nucleus, and the approaching end of the life of the cells.

Flemming says, "Fragmentation of the nucleus, with and without subsequent division of the cell, is universally a

process in the tissues of Vertebrates which does not lead to the physiological multiplication and reproduction of cells, but, on the contrary, represents where it occurs a degeneration or aberration, or perhaps, in many cases, is subservient to the metabolism of the cell by increasing the periphery of the nucleus."

Ziegler (65), who quotes the above passage from Flemming's work, discusses in detail some of the many instances of amitotic nuclear division, and comes to similar conclusions. He says that amitotic division of the nucleus always indicates the end of the series of divisions, and considers it hardly probable that nuclei which have arisen by amitotic division will ever again divide by mitosis.

If Flemming, Ziegler, and those who agree with them are right, then it is clear that the oosperm nucleus does not and cannot fragment. It must divide regularly by karyokinesis. But Ziegler's views are, it seems to me, altogether untenable. By simply denying, or passing over in silence, many instances of fragmentation of the nucleus, which do not support his views, he has given undue weight to mitosis, and leaves an unsatisfactory gap in the list of cases which support his theory.

Verson (56), Frenzel (12), and Löwit (40) have, since the publication of Ziegler's paper, called attention to cases of amitotic division of the nucleus which are most certainly not followed either by nuclear degeneration or by a cessation of cell multiplication.

A review of the recent literature of cell division shows that the cases given by these authors may be supplemented by many others, and, indeed, leads one to a conclusion quite different from that of Ziegler and Flemming, namely, that indirect nuclear division rarely occurs unless it is preceded by or accompanied by some partial or complete segmentation or division of the surrounding cell substance.

It is undoubtedly true that in many cases amitotic fragmentation of the nucleus is followed by its degeneration and the death of the cell. The numerous examples quoted by

Ziegler prove that this is the case. But I shall endeavour to show that we are by no means justified in assuming that amitotic fragmentation is a sign of degeneration.

In the first place, it can be shown that there is considerable evidence for believing that the oosperm nucleus of some ova does not divide by normal karyokinesis, but does split up amitotically into a large number of minute fragments.

I have already described (17 and 18) such a process of fragmentation in the case of Millepora, Allopora, and Disticho-pora, but the following considerations prove that the same is probably true of many other eggs.

Cœlenterata.—In the development of Alcyonium the germinal vesicle entirely disappears, and no traces of the karyokinetic division of the oosperm nucleus can be found. Kowalewsky[1] (37) gives a figure of the ovum without any nucleus, but my own observations show that at a stage corresponding to the one he figures the nucleus is in the form of a number of minute fragments scattered through the substance of the ovum.

The failure to find karyokinetic division of the oosperm nucleus cannot be attributed to imperfect methods of pre-servation or staining, because young embryos, preserved and stained in precisely the same way as the fertilised ova, exhibit beautiful and typical karyokinetic figures.

The early stages in the development of Gorgonia cævolini, described by G. von Koch (36), seem to be precisely similar to those of Alcyonium. In the unfertilised ovum there is a large germinal vesicle containing an excentrically placed germinal spot, but in the eggs that he believed to be fertilised there was no nucleus. "Ihre Structur weicht von der des unbefruchteten Eies wesentlich ab. Es fehlt nämlich vor allem der Kern, von dem ich keine Spur mehr auffinden konnte." The fact that von Koch, after carefully examining over a hundred series of sections through fertilised ova, could find neither traces of segmentation nor the division of the oosperm nucleus, suggests

[1] As Kowalewsky's paper is written in the Russian language I am unable to read it.

very forcibly that the ovum of Gorgonia does not segment at first, and that the oosperm nucleus fragments as it does in Alcyonium.

Arthropoda.—In the development of Peripatus capensis, Sedgwick (51) has described the division of the ovum into two blastomeres, and the large and easily seen karyokinetic figures which mark the first division of the oosperm nucleus. The fertilised ovum of Peripatus novae-zealandiae, however, does not segment, and Miss Sheldon (53) was unable to find any karyokinetic figures in the divisions of its nucleus.

It is a very striking fact in support of my views that in two species of the same genus we should find such· a well-marked difference in this respect, the ovum that does segment showing clear and unmistakable nuclear mitosis, and the ovum that does not segment showing no signs of karyokinesis.

But this is not the only example of the relation between the segmentation and the division of the nucleus.

In a recent paper on the "Embryology of the Macroura" Herrick (6) states that it is a rule with the decapod Crustacea that the nuclei of the segmenting eggs divide with karyokinesis. There is an exception to this rule, however, in the case of Alpheus minus. "The fertile egg of A. minus is pervaded with a remarkably fine reticulum which encloses spherules of minute and uniform size. The nucleus is central or nearly so, and consists of an ill-defined mass of protoplasm, in which a fine chromatin network is suspended. In the next phase the nucleus is elongated and about to divide. Division appears to be direct and irregular. At a somewhat later stage the phenomena of the most interest occur. Each product of the first nucleus has developed a swarm of nuclear bodies which seem to arise by fragmentation. These bodies take the form of spherical nuclei in clear masses of protoplasm. . . . In the last stage obtained the whole egg is filled with several hundred very large elements, which are descended more or less directly from some of the nuclear

bodies just considered, but the intermediate stages have not been considered."

In the species Alpheus Saulcyi and Alpheus hetero-chelis (two varieties) the segmentation is normal and regular, of the centrolecithal type, and the division of the nuclei indirect. In Alpheus minus alone is the segmentation extremely irregular and the nuclear division direct.

Among Myriapoda we find that the ovum of Julus terrestris is very similar in many respects to that of the Stylasteridæ. There are no signs of segmentation, and there is no formation of cells until the time when the epiblast is formed. Heathcote (20), who carefully studied the early stages in the development of this species, could not find any signs of karyokinesis in the first divisions of the oosperm nucleus.

There is, according to Kingsley (33), a disappearance of the germinal vesicle of the American Limulus, and it is a suggestive fact that Kishinouye (35), in his careful paper on the development of Limulus longispina, does not refer to the first nuclear divisions.

It is possible that there may be a fragmentation of the oosperm nucleus in the ova of some other Arachnida.

In the development of many Insecta there are many facts that point to the conclusion that the oosperm nucleus fragments.

It is noteworthy in the first place that, notwithstanding the fact that several excellent embryologists have carefully studied the development of the common blow-fly, not one of them has been able to give a satisfactory account of the first division of the oosperm nucleus.

Blochman (3), who figures the spindles of the nuclear divisions in the formation of the polar bodies, and also the spindles of the nuclear divisions of the later stages of embryonic development, did not apparently observe the first division of the oosperm nucleus. He says, " Als erste Theilung des Eikernes kann man die Bilder wohl nicht auffassen, weil, wie ein Blick auf die späteren Figuren zeigt, bei Theilungen die

Tochter kernplatten stets so fort weit aus einander rücken."
Henking (21), too, was unable to find the first division of the
oosperm nucleus of Musca.

Now, in Musca, and in many other insects in which the early
divisions of the oosperm nucleus have not been made out, the
occurrence " of free nuclear formation " has been described in
the young embryo.   Whence come these free nuclei?   It can
hardly be believed that they are actually formed in the cell
substance from something that is not directly derived from a
pre-existing nucleus.   All the evidence of modern histology
tends to prove that nuclei are derived from nuclei, and nuclei
only, and it is only reasonable to suppose that the so-called
"free nuclei" of insect embryos are formed by the growth or
fusion of fragments of the oosperm nucleus.

The evidence in support of this hypothesis is not the purely
negative evidence of the absence of any direct proof of mitotic
division of the first nuclei, but the fusion of minute chromatin
bodies to form larger ones has actually been observed by
Henking (23) in the embryos of Pieris, Pyrrochoris, and Lasius.

But it is extremely probable that fragmentation of the
oosperm nucleus is of very frequent occurrence in the eggs of
insects.   In many cases, both in large yolk-laden eggs and in
small yolk-free eggs, the fertilisation is followed by the
appearance of numerous nuclei in the substance of the egg.

In Neophalax concinnus, one of the Phryganids, the
division of the oosperm nucleus was not observed by Patten
(46), and the following is his account of the early stages :—
" Within ten or twelve hours after oviposition—the time
varying with the temperature—a clear space makes its ap-
pearance at the surface of the egg, and gradually increases
until it has attained the breadth of the future blastoderm.
In this layer, which has been called the ' blastema,' the pro-
toplasm has, under ordinary conditions, a very homogeneous
appearance, with occasionally lighter, less refractive spots,
which appear like vacuoles, but in which, when observed more
closely and under slight pressure of a cover-glass, or especially
when treated with a very little acetic acid, faintly marked

nuclei make their appearance in greater or less numbers according to the more or less advanced stage of the blastema."
It is extremely improbable, if the minute nuclei in the blastema could be observed by the simple method of treatment with acetic acid, that the karyokinetic divisions of the large oosperm nucleus, if they really occur, would have been overlooked.

Many other instances could be given from the writings of naturalists during the last twenty years of the failure to trace the divisions of the oosperm nucleus in insect eggs, and of the occurrence of "free nuclear formation" in the eggs after fertilisation; but in many of these instances it might be urged that sufficient patience was not exercised, or that the methods of preservation and staining were imperfect.

An important paper has, however, been recently published by Henking (23) containing an extremely elaborate account of his investigations upon many different species of insects carried on with the aid of the best modern methods of research. It would take me far beyond the limits of this paper to give even an outline sketch of Henking's important results, but a brief reference to some of the points bearing upon the subject of this essay must be made.

In Pyrrochoris, one of the Hemiptera, Henking finds that in the formation of the polar bodies the nucleus divides by a process of karyokinesis, the chromatin bodies being of considerable size and definite in number.

After fertilisation a new spindle is formed with the chromosomes arranged in an equatorial plate, but before the division is completed the chromosomes disappear. Later on the chromosomes reappear in the form of extremely minute and numerous granules, which fuse together into threads, and arrange themselves in the equatorial plate of a new spindle.

Similarly, in Agelastica alni, a Coleopteran, the chromatin entirely disappears after the division of the segmentation nucleus.

In the Hymenopteran Lasius the chromatin of the first two segmentation nuclei completely disappears, and when the

nuclei are about to divide again reappears in the form of extremely minute granules, which fuse together to form the chromosomes of the next division.

A similar disappearance has been described in the unfertilised egg of Rhodites, and in this form there is no membrane surrounding the nuclei.

These researches prove, then, that in some insects there is a "disappearance" of the chromatin substance of the nucleus after its first division.

To what is this disappearance due? Henking thinks that it is due to some chemical change in the chromatin substance, as in some cases the outline of the chromosomes may be observed after the disappearance of the colouring matter. Nevertheless it is a fact that commonly the chromosomes lose their compact form during the colourless stage, and become very finely divided. We can attribute the disappearance, then, partly to the change in the chemical character of the chromatin, and partly to the very minute and scattered condition of its elements.

Further, in some cases (Rhodites) not only does the chromatin disappear, but also the membrane surrounding the nuclear area, so that we have (as in Distichopora, &c.) a condition in which the nucleus is practically indistinguishable from the surrounding protoplasm.

It is during this condition that some of the nuclear fragments may be distributed through the substance of the ovum, and give use to the nuclei of the so-called "free nuclear formation" by subsequent fusion.

It must be obvious to anyone who carefully studies Henking's figures that in many insects the spindle of the first division of the oosperm nucleus is very irregular, that the chromosomes are not always arranged with the same mathematical precision that they are in typical karyokinetic figures, and further, that in consequence of the disappearance and extremely fine division of the chromatin substances there are still some steps in the nuclear divisions at the commencement of development which have not been satisfactorily traced.

We may go further than this, though, and say that some of
Henking's figures, such as figs. 335, 336, and 337 of Lasius,
can only be interpreted on the supposition that the nucleus has
fragmented. The little clusters of chromatin granules, of very
irregular size and indefinite arrangement, that are here
figured scattered through the substance of the ovum, cannot be
considered to be the product of regular mitosis.

It seems to be extremely probable that in the group of
insects we have a series of stages intermediate in condition
between regular mitotic division of the oosperm nucleus or its
immediate successors and irregular fragmentation.

In Aphis (Will, 62) we may have regular karyokinesis at all
stages of the segmentation, the chromosomes being divided
into two equal halves at each division of the nucleus; but in
Musca, in Lasius, and perhaps in several others in which the
earliest stages are passed through with great rapidity, the
nuclei fragment with greater or less irregularity.

That the occurrence of karyokinesis is in some way dependent
upon forces manifesting themselves in the cell substance of
the ovum and acting upon the nuclei is rendered probable (1) by
the fact that in Aphis, where the nuclei divide by karyokinesis
in all stages, there is, as Will points out, a distinct aggregation
of protoplasm round the nuclei, and (2) by the fact that in
nearly all insects the karyokinetic figures of the nuclear
divisions that take place in the formation of the polar bodies
are much more regular and constant than they are in the early
stages of development.

But I shall discuss this point and general significance of
mitosis in greater detail later on.

That a similar process of fragmentation of the oosperm
nucleus may also occur in some Vertebrata seems to be probable
from the recent researches of Kastschenko (31) upon Elasmo-
branchs. It must be remembered that the early stages of the
development of Elasmobranchs and birds have been carefully
studied by numerous observers for the last twenty years, and
although the karyokinetic spindles in the developing blasto-
derm and its surrounding yolk have been described by nearly

all of them, we have not received any account of the first
division of the oosperm nucleus.

It is quite unreasonable to suppose that all these observers
would have overlooked a nuclear division—which we might
expect, if it exists at all, to be the largest and most conspicuous
of the whole series. Nor can we suppose that the methods of
preservation or staining was so consistently bad at the first
stage as to prevent the observation of the figure, and so fre-
quently good in the later stages as to show the whole process of
karyokinesis clearly and distinctly.

Now Kastschenko (31) shows that in Elasmobranchs a
number of nuclei appear in the blastoderm and the surround-
ing yolk before the formation of the segmentation furrows,
which appear not in regular sequence, but simultaneously and
irregularly. "Die bekannte regelmässige Reihenfolge des
Erscheinens des Segmentationsfurchen existiert bei Selachiern
fast gar nicht. Nur in seltenen Fällen bemerkt man das
ursprüngliche Erscheinen einer Segmentationsfurche, welcher
dann gleichzeitig mehrere andere unregelmässig sich kreuzende
folgen. In den meisten Fällen aber erscheinen schon vom
Anfang an mehrere Segmentationsfurchen gleichzeitig und
somit zerfällt die Keimscheibe direct in mehrere verschieden
grosse Segmentationskugeln, welche sich dann weiter aber nicht
gleichzeitig theilen."

We have, then, at the commencement of the development of
the Elasmobranch a multinucleated plasmodium, and Kast-
schenko is of opinion that all the nuclei of this plasmodium are
formed by repeated divisions of the first segmentation nucleus·
But, like all his predecessors, Kastschenko was apparently
unable to observe these repeated divisions of the first nucleus,
and it seems extremely probable that in Elasmobranchs, as in
insects, Hydrocorallines, and others, we have at this stage a
true process of nuclear fragmentation.

I have already called attention to the fact that in all of these
cases in which the fragmentation of the oosperm nucleus
probably occurs the ovum does not segment immediately after
fertilisation ; that there is, in fact, for a time in the early em-

bryonic development a multinucleated plasmodium without any definite cell walls or cell areas.

There can be little doubt, I think, that in all holoblastic eggs, such as those of Echinoderms, worms, Amphioxus, &c., the first segmentation is accompanied by typical karyokinetic division of the nucleus.

We may go further than this, and say that in many meroblastic eggs the first divison of the oosperm nucleus is also an indirect one.   Vialleton (57) and Watase (59) have observed this division in the egg of Cephalopods, and Oppel (45) has observed it in the egg of the lizard, Anguis fragilis. But in both these cases the segmentation furrows occur regularly and in sequence from the commencement of development, and we have, consequently, evidence that the same forces are at work in the protoplasm as those which produce the more or less complete blastomeres of holoblastic eggs.   Even in those eggs of insects in which the nuclei are known to divide by karyokinesis there is evidence of the drawing together of the protoplasm along certain lines of force in the "plasmatische Strahlungen" of Henking, which surround the nuclei.

But if there is any truth in the view that I have here put forward, that karyokinesis is primarily due to the forces which bring about cell division, and that in those cases in which cells or cell areas are not formed the nucleus may fragment or divide directly in some other way, then we should expect to find some further evidence of fragmentation of the nucleus in other tissues.   There is ample evidence of this in other tissues.

In the formation of the spores in Protozoa the nucleus of the parent cell often divides long before there is any division of the cell protoplasm, and in nearly all such cases division of the nucleus is direct.   In some cases the nucleus disappears, and it is probable, as in the case of the oosperm nucleus quoted above, that this may be due to the extremely fine division of the chromosomes and fragmentation.

I will give just a few examples to illustrate these points.

Wolters (64), in describing the conjugation of Monocystis magna and agilis, says, " Kurz nach erfolgter Encystirung

soll der Kern, respective die Kerne der beiden Copulanten sehr undeutlich werden. Sie entziehen sich zuletzt dem beobachtenden Auge ganz und sind im Inhalte der ausgequetschten Cyste nicht mehr zu finden." The author figures, it is true, an achromatic spindle in the encysted forms after the extrusion of the polar bodies, but the chromatin bodies are very minuteand irregularly scattered through the substance of the protoplasm. "Es gelangzwar nicht," he says, "eine zusammenhängende Reihe von Bildern für die Constatirung der mitotischen Theilung an den Sporogonien zusammen zustellen, doch liess sich mit Sicherheit constatiren, dass die Kernmembran an manchen Kernen der ungetheilten Sporogonie geschwunden war und die färbbare Substanz in zwei, durch einen grösseren Zwischenraum getrennte Reihen angeordnet war."

But the evidence in favour of a process of fragmentation of the nucleus seems to be much more conclusive in the case of Clepsidrina blattarum (Wolters, l. c.). In this form nuclei are found " in denen unzählige kleine chromatische Körner lagen, wie es schien regellos, ohne besondere Anordnung vertheilt. Allen bisheran geschilderten Kernformen war dagegen eine scharf contourirte Kermembran gemeinsam. Im Gegensatz da zu stehen Formen, die ebenfalls häufig beobachtet wurden, welche einer solchen Membran entbehrten. Der Kern breitet sich sternförmig mit seinen Fortsätzen in die Leibessubstanz des Thieres aus und steht mit dem protoplasmatischen Gefüge derselben in directen unterbrochenen Zusammenhange."

This account of the fragmentation of the nucleus of Clepsidrina blattarum is confirmed in all its essential details by the more recent work of Marshall (40 a), who was unable to find at any time any traces of karyokinesis. A very similar account is given by Schneider (49) of the division of the nucleus of Klossia.

It may be that in some forms, such as the Gregarina irregularis of Holothuria nigra (Minchin, 43), a regular form of division with mitosis does occur, but this does not detract from the importance of the fact that in many

Gregarines which form during encystment a vast number of spores, no karyokinetic figures can be observed.

Many years ago Hertwig (24) described a curious method of the fragmentation of the nucleus without karyokinesis in the spore formation of Thalassicola, and more recently Brandt (4) was unable to find karyokinesis in the divisions of the nucleus to form the nuclei of the spores of the Sphærozooids.

Gruber (16) has described several instances among the ciliate Infusoria in which the nucleus apparently fragments into extremely minute granules, which become scattered through the protoplasm of the body and collect again into lumps.

Jickeli (29) has described fragmentation of the nucleus of Stylonychia, Paramœcium, and other Ciliata.

Quite recently, too, Lister (39), in his researches upon Orbitolites, has not been able to discover any signs of karyo-kinesis in the division of the nuclei.

There is probably, too, a method of fragmentation in the spermatogenesis of many animals. I have myself carefully examined the earliest divisions of the nucleus of the sperm mother-cell of Millepora, Allopora, Distichopora, and Alcy-onium, and I can find no trace of karyokinesis. It is, in fact, only in a few exceptional cases, such as Ascaris (Hertwig, 25), where the cell outlines of the spermatocytes are very early delineated, that karyokinesis has been observed in the division of the nuclei of the sperm mother-cells.

Verson (56) shows that in Bombyx mori the primordial cells have at first a giant nucleus, which divides amitotically to form numerous secondary nuclei, and these divide mitotically to form the nuclei of the Spermatids.

Bolles Lee (38) found amitotic division of the nuclei of the spermatogonia of Chætognatha and Nemertines and regular karyokinesis in the division of the nuclei of the spermatocytes.

Dostojewski found the same thing in the spermatogenesis of Amphibia (see Waldeyer, 58, p. 39), and other examples could be quoted from the writings of La Valette St. George, Gilson, Sabatier, and others (see Waldeyer, 58, p. 39).

In some Annelid worms the nucleus of the spermatogonium disappears, and there is no evidence at present that the nuclei of the spermatocytes are derived by repeated mitotic divisions of this nucleus (Jensen, 28, and others). In the recent work on spermatogenesis, by Pictet (47) no mention is made of the manner in which the nuclei of the spermatogonia divide in Polychætes.[1]

A study of the literature of spermatogenesis shows that when there is a distinct division of the protoplasm to form the spermatocytes or spermatogonia, distinct karyokinesis of the nuclei may generally be seen; but when, on the contrary, multinucleated cells are formed, which eventually give rise to the spermatocytes, the nucleus of the spermatogonia either disappears or divides amitotically.

It is not necessary for me to discuss in detail the numerous cases of indirect fragmentation of the nucleus that have been described by Arnold in his numerous papers in 'Virchow's Archiv' and the 'Archiv für mikroscopische Anatomie,' by Werner (61), Schottlaender (50), Hess (26), Geelmuyden (13), Beltzow (2), Ströbe (54), Göppert (15), and others. Many of these cases are those of the nuclear division of giant-cells, and I believe I am quite correct in saying that in all of them the fragmentation of the nucleus is not immediately followed by cell division.

The general conclusions to be drawn from the evidence before us are — 1. That fragmentation of the nucleus is a normal method of nuclear division, and is not always a sign of pathological change. 2. That in many of the instances in which the nucleus is supposed to disappear there is, as a matter of fact, minute fragmentation. 3. That fragmentation only occurs where there is no cell division; and 4. That karyokinetic division of the nuclei is caused by the forces in the cell protoplasm which bring about the division of the cytoplasm.

That there may be many forms of nuclear division inter-

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[1] It is a noteworthy point that O. von Rath (48), who believes that the nuclei of the spermatogonia and spermatocytes always divide mitotically, does not refer at all in his paper to the spermatogenesis of Polychætes.

mediate in character between fragmentation and bipolar karyokinesis seems to be probable from the discovery of pluripolar mitosis in the inflamed cornea by Schottlaender (50), and other atypical nuclear divisions in the spleen of the white mouse by Arnold (1), &c.

We have, then, a series of phenomena in the division of nuclei, with typical karyokinesis at one end and direct fragmentation at the other. The occurrence of any one kind or the other is, in my opinion, determined by the forces which act simultaneously upon nucleus and cell plasm. If these forces are of such a kind as to drag the cell plasm into two equal halves, the nucleus is also dragged into two equal halves with mitosis; if, on the other hand, the forces are irregular and act from many centres at the same time, the nucleus fragments irregularly.

These views seem to me to be supported by the statement of Flemming (11) quoted by Sedgwick, that " the first change observable in a cell whose nucleus is about to divide is in the extra-nuclear protoplasm," and by Bürger's (7) recent conclusions concerning the meaning of the spheres of attraction.

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DESCRIPTION OF PLATE IV,

Illustrating Dr. Sydney J. Hickson's paper on the "Development of Distichopora."

FIG. 1.—Young ovum of Distichopora, situated in the cup-shaped trophodisc (*tr.*). The germinal vesicle, *G. v.*, is situated near the centre of the ovum.

FIG. 2.—Germinal vesicle of the same stage, showing the vacuoles in the nucleolus.

FIG. 3.—Germinal vesicle of the ovum of Distichopora, migrating from the centre to the periphery. The membrana limitans becomes obscure over the pseudopodial processes.

FIG. 4.—A peculiar condition of the germinal vesicle, observed in only one preparation.

FIG. 5.—A germinal vesicle, with chromatin granules arranged in a row.

FIG. 6.—Germinal vesicle, containing numerous minute chromatin granules situated at the periphery of the ovum.

FIG. 7.—A stage showing the disappearance of the inner part of the membrana limitans.

FIG. 8.—A stage showing the complete disappearance of the membrana limitans.

FIG. 9.—Section of a young embryo which shows only two large nodes of protoplasm, each of them containing a few deeply staining granules. The yolk is omitted from the lower part of the section in order to show the loose protoplasmic mesh-work which pervades the embryo.

FIG. 10.—A later stage in the development, showing several nodes of various sizes, some with nuclei, some without.

FIG. 11.—A stage in the development corresponding to that of Fig. 10, to show the relation of the nuclei to the yolk. Each nucleus is situated in a small protoplasmic area or node, and the yolk granules close to it are extremely small.

FIG. 12.—The same stage as Fig. 10, showing the different phases in the formation of the nuclei. The details of the yolk are omitted.

Fig. 13.—A section of a young embryo, which shows yolk segmentation.

Fig. 14.—A section through an older embryo, the yolk being omitted, showing the first stages in the formation of the ectoderm (*ect.*). *ec.* Ectoderm. *en.* Endoderm of the gonophore.

Fig. 15.—A section through a still older embryo, showing a later stage in the formation of the ectoderm and its connection with the central endoderm plasmodium.

Fig. 16.—A solid planula of Distichopora, just before it escapes from the gonophores.

Fig. 17.—A small portion of the endodermic plasmodium more highly magnified. Some of the smaller yolk granules are omitted.

Fig. 18.—*a, b, c, d, e.* Six stages in the division of the nuclei of the ectoderm.

Fig. 1.

G.v.
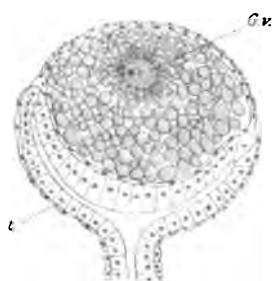
Fig. 2.

Fig. 4.

Fig. 3.

Fig. 7.

Fu
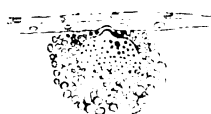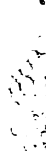
Fig. 10.
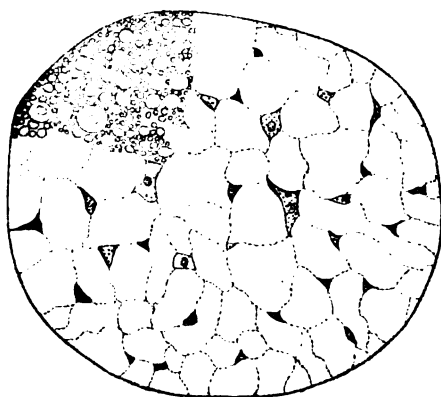
Fig. 11.
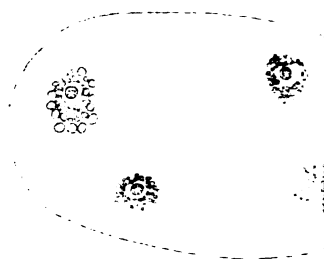
Fig. 12.
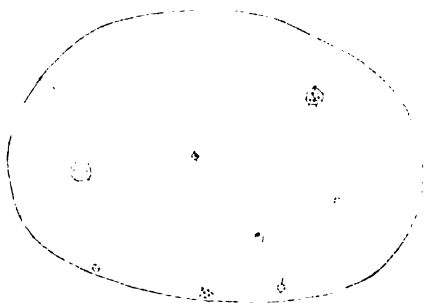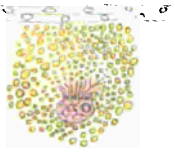
Fig. 13.

Fig. 5.

Fig. 6.

Fig. 18.

Fig. 17.

Fig. 9.

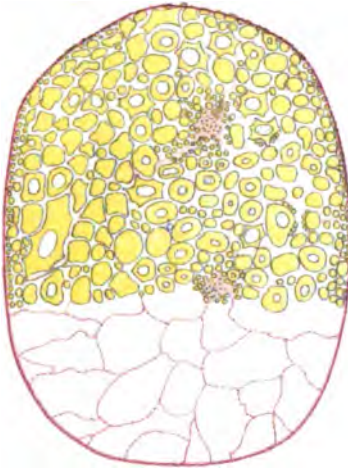Fig. 8.

Fig. 16.

Fig. 15.

Fig. 14.

ec.

en.

ect.

ect.
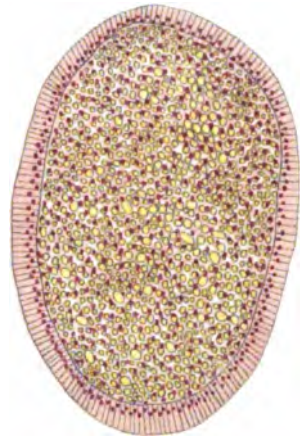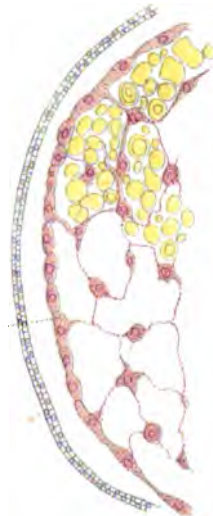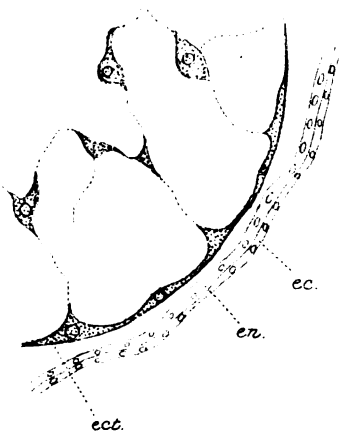
On the Law of Development commonly known as von Baer's Law; and on the Significance of Ancestral Rudiments in Embryonic Development.

By

Adam Sedgwick, M.A., F.R.S.

THE generalisation commonly referred to as v. Baer's law is usually stated as follows:—Embryos of different members of the same group are more alike than the adults, and the resemblances are greater the younger the embryos examined. It appears to be pretty clear that v. Baer held some such view as this,[1] and there can be no doubt that it is a view which is largely taught at the present day.[2] In fact, I think it is safe to say that all zoologists are brought up with this view as one of the fundamental postulates of their science.

It will be the object of the following pages to show that this view is not in accordance with the facts of development. V. Baer based his view mainly upon the study of Vertebrate embryos; and it will be convenient for us, in criticising him, to begin with an examination of this group. We may also, in the first instance, follow v. Baer in another point, viz. in limiting ourselves to the consideration of embryos as opposed to larvæ. Embryonic development and larval development take place under entirely different conditions, and in order to obtain clear ideas they must be considered apart in treating

[1] Vide 'Ueber Entwickelungsgesch. d. Thiere,' part i, pp. 221, 223, and 224.

[2] Vide Darwin in 'Origin of Species,' p. 364, 6th ed.; and Balfour, 'Comp. Embryology,' vol. i, p. 2.

this subject. They have not as a rule been clearly distinguished, and facts based on a study of larvæ have sometimes been assumed to hold true for embryos without further examination; and this practice has, as I hope to show, given rise to errors which have prevented our arriving at a clear understanding of the subject.

It is, of course, impossible to examine fully all the stages of all Vertebrate embryos. In the comparison necessary for the criticism I am making it will be convenient to limit ourselves to typical cases, and I propose to consider (1) the embryos of animals widely divergent ; (2) the embryos of animals which are closely allied in the adult state. If it is found that in neither of these cases is the law of v. Baer followed, then I think we may reason that there is, to say the least of it, a strong probability that it will be found not to hold true for intermediate cases.

(1) Embryos of divergent classes of the Craniate phylum. The examples I have chosen are the fowl and dog-fish.

The fowl and the dog-fish in the adult state live under entirely different conditions; whereas in the embryonic phases the conditions are very similar, both being developed within an egg-shell at the expense of ovarian yolk and surrounding albumen.

According to the law of v. Baer these embryos ought to be closely similar in the young stage.

Do these embryos, developing under similar conditions, conform to the law ? Superficially, clearly not. There is no stage of development in which the unaided eye would fail to distinguish between them with ease—the green yolk of the one, the yellow yolk of the other; the embryonic rim and blastopore of the fish, the absence of these in the chick; the six large gill-slits bearing gills on the one hand, the four rudimentary clefts on the other; the small head, straight body, and long tail, as opposed to the enormous head, cerebral curvature, short tail, and so on. A blind man could distinguish between them.[1] These embryos are not closely similar,

[1] I do not feel called upon to characterise the accuracy of the drawings of

but it is maintained that the law is justified by certain remark-
able features of embryonic similarity which the adults do not
exhibit, and of which the most important are the presence in
the chick of pharyngeal clefts, a tubular piscine heart, and a
similarity in the arrangement of the cardiac arterial system,
a cartilaginous endo-skeleton, oro-nasal grooves, and a noto-
chord.   Now I freely admit that these are striking similarities,
but I question whether they are sufficient to justify the law of
v. Baer.   By themselves, no doubt, they would be sufficient to
justify that law ; but are there no differences to set off against
them ?   Are there no differences of a morphological value, as far-
reaching and as striking as these similarities ?   Let us clearly
understand the question at issue.   V. Baer's law, as applied to
the present case, may fairly be held to mean, if it has any
meaning at all, that whereas the differences between the adults
are large and important differences of class value, the differ-
ences between the embryos are slighter and unimportant, and of
less than class value.   Now in no single member of the group
Craniata is the mesoderm of the head segmented.   According
to our present morphological knowledge, the discovery of an
animal with cranial segments would be a very remarkable one,
and would, we might confidently predict, require the establish-
ment of a class at least separate from all other Craniate
classes—such is our estimation of the importance of this
feature.   And if to this character was also added the presence
of a cœlomic sac close to the eye, of another in the jaw, and of
a third near the ear ; of an aperture of communication between
the neural canal and rectum, of kidney tubules opening into
the muscle-plate cœlom as well as into the perivisceral cœlom,
of a Müllerian duct opening into the front end of the Wolffian,
I do not think that any anatomist would have any doubt about
the matter.   Now it is precisely in these points, amongst

embryos of different classes of the Vertebrata given by Haeckel in his popular
works, and reproduced by Romanes and, for all that I know, other popular
exponents of the evolution theory.   As a sample of their accuracy, I may
refer the reader to the varied position of the auditory sac in the drawings
of the younger embryos.

others, that the embryo dogfish differs from the embryo chick.
I am quite aware that arguments tending to reduce the
classificatory value of the embryonic differences I have just
enumerated might with more or less plausibility be adduced.
But one thing at a time. I am at present dealing solely with
the importance of the anatomical resemblances and differences
between the embryos; and I think I have shown, as far as it
can be shown, that they have, if judged by standards used
when comparing adults, at least as great an importance as the
resemblances between the same embryos—the differences, like
the resemblances, relating solely to the embryos, and not
existing in the adults. V. Baer's law then falls to the ground,
and must be replaced by another law, which is as follows:—
Embryos of different members of the same group often resemble
one another in points in which the adults differ, and differ from
one another in points in which the adults resemble; and it is
difficult, even if possible, to say whether the differences or the
resemblances have the greater zoological value (because we
have no clearly defined standard of zoological value).

It will probably be urged here by my reader—Are you not
beating the air in a vain warfare of words and unessentials of
which we were all aware, and trying to kick up a cloud of dust
by which to obscure the essential point, viz. that embryos
pass through, incompletely if you like, stages of structure
permanent in lower members of the same group? To such a one
I reply, that I am as keenly alive to the importance of the
essential point as he is, but that I differ from him in being
dissatisfied with the explanation which is at present given of it,
and that I am convinced that the form in which this pheno-
menon is referred to in v. Baer's law has led to the acceptance
of an imperfect explanation of the embryonic phase in animal
development.

(2) But before I come to that point I have to consider
the case of the embryos of closely allied animals. If v.
Baer's law has any meaning at all, surely it must imply that
animals so closely allied as the fowl and duck would be indis-
tinguishable in the early stages of development; and that in

two species so closely similar that I was long in doubt whether
they were distinct species, viz. Peripatus Capensis and
Balfouri, it would be useless to look for embryonic differ-
ences : yet I can distinguish a fowl and a duck embryo on
the second day by the inspection of a single transverse section
through the trunk, and it was the embryonic differences between
the Peripatuses which led me to establish without hesitation the
two separate species.   But it is not necessary to emphasise
further these embryonic differences ; every embryologist knows
that they exist and could bring forward innumerable instances
of them.   I need only say with regard to them that a species
is distinct and distinguishable from its allies from
the very earliest stages all through the develop-
ment, although these embryonic differences do not
necessarily implicate the same organs as do the
adult differences.

If I have laid great stress—some may think undue stress—
upon the inadequacy of v. Baer's law, I have done so be-
cause of the importance which is at the present day attached
to this law by teachers of zoology.   In support of this, I may
quote the words of three of the greatest teachers of zoology of
this or of any other age—words which show that they at any
rate considered that the law correctly represented the facts.

Darwin, in the 'Origin' (p. 387, 6th ed.), says:—"So
again it has been shown that generally the embryos of the
most distinct species belonging to the same class are closely
similar, but become, when fully developed, widely dissimilar.
A better proof of this latter fact cannot be given than the
statement by v. Baer that the embryos of Mammalia, of
birds, of lizards, and snakes, probably also of Chelonia, are in
their earliest states exceedingly like one another, both as a
whole and in the mode of development of their parts ; so much
so, in fact, that we can often distinguish the embryos only by
their size.   In my possession are two little embryos in spirit,
whose names I have omitted to attach, and at present I am
quite unable to say to what class they belong.   They may be
lizards or small birds, or very young Mammalia, so complete

is the mode of formation of the head and trunk in these animals."

This, I think, shows quite clearly Darwin's view of the matter.

Huxley, in his 'Man's Place in Nature,' says:—"The history of the development of any other Vertebrate animal—lizard, snake, frog, or fish—tells the same story. There is always, to begin with, an egg having the same essential structure as that of the dog; the yolk of that egg undergoes division or segmentation, as it is called, the ultimate products of that segmentation constitute the building materials for the body of the young animal; and this is built up round a primitive groove, in the floor of which a notochord is developed. Furthermore, there is a period in which the young of all these animals resemble one another, not merely in outward form, but in all essentials of structure, so closely, that the differences between them are inconsiderable, while in their subsequent course they diverge more and more widely from one another."

The Significance of Ancestral Rudiments in Embryonic Development.

The existence of a phase at the beginning of life during which a young animal acquires its equipment by a process of growth of the germ, is of course intelligible enough. We see such a phase in the formation of buds, and in the sexual reproduction of both animals and plants. The remarkable point is that while in most cases this embryonic growth is a direct and simple process—e.g. animal and plant buds, embryonic development of plant seeds—in some cases—e.g. most cases of sexual reproduction of animals—it is a circuitous one, and the embryonic phase shows stages of structure which seem to possess a meaning other than that of being merely phases of growth.

As is well known, the explanation which is given of this circuitous course of embryonic development is that we are dealing with a special case of the law of heredity—"each

organism reproducing the variations inherited from all its ancestors at successive stages in its individual ontogeny" ('Comp. Emb.,' vol. i, p. 3).

"These two principles, namely, that slight variations generally appear at a not very early period of life, and are inherited at a corresponding not early period, explain, as I believe, all the above specified leading facts in embryology." (Darwin, 'Origin,' p. 392, ed. vi.)

But this explanation, though good as far as it goes, is not entirely satisfactory, because it fails to explain (without further qualifications) the majority of cases (animal and plant buds, embryonic development of seeds) in which ontogeny presents no ancestral traces; it is at variance with the fact that in many cases variations which affect the adult have affected the whole of embryonic development (see below); and it does not enable us to understand why some organs, e.g. gill slits, have been retained in embryogeny, whereas other organs which have much more recently disappeared, e.g. teeth of birds, fore-limbs of snakes, have been entirely lost. It assumes that the repetition of ancestral characters in embryogeny is the intelligible rule; and that their omission is the exception which requires explanation whenever it occurs. This assumption is not warranted by the fact above indicated that in the vast majority of ontogenies there are no phylogenetic traces, nor by the consideration that a number of important organs, such as teeth and hand-claws in birds, limbs in snakes, gill-clefts in fishes, have recently disappeared without leaving a trace in ontogeny.

In fact the balance of evidence appears to me to point most clearly to the fact that the tendency in embryonic development is to directness and abbreviation and to the omission of ancestral stages of structure, and that variations do not merely affect the not-early period of life where they are of immediate functional importance to the animal, but, on the contrary, that they are inherent in the germ and affect more or less profoundly the whole of development.

I am well aware that in holding this opinion I am running

counter to the great authority of Darwin. In the chapter
from which the above quotation was taken he gives many facts
and arguments in favour of the view that slight variations
generally appear at a not very early period of life, and are
inherited at a corresponding not early period. He admits that
larger variations—monstrosities—do affect the embryo at a
very early period, but he thinks that slight variations do not.
Without considering the difficult question as to where the line
should be drawn between a slight variation and a monstrosity,
I may merely point out that Darwin's evidence is largely based
upon the experience of breeders that it is impossible to tell
until some time after birth what will be the merits or demerits
of their young animals. In mitigation of the force of this fact
it must be remembered that a successful breeder is a highly
skilled man—that he possesses powers of observation greater
than the ordinary—that his success depends upon his ability
to see points which escape the eye of other people. If the
points for which the mature animal is selected are thus
difficult of observation, can we wonder if it is beyond the
power of man to see them when the animal is immature, and
the relative sizes of the parts of the animal, and its whole
appearance, are so different? In support of this way of looking
at the matter I would urge that when the variation is large
and of a nature to be easily observed, it can—in a great
many instances at any rate—be detected all through develop-
ment.

The evidence is of this kind :—(1) Organs which we know
have only recently disappeared are not developed at all in the
embryo. For instance, the teeth of birds, the fore-limbs of
snakes, reduced toes of bird's foot (and probably of horse's
foot), the reduced fingers of a bird's hand. These are instances
which readily occur; I have no doubt that many others might
be quoted by anyone giving attention to the matter. (2) Organs
which have (presumably) recently become reduced or enlarged
in the adult, are also reduced or enlarged in the embryo.
Many examples of this might be given, and it is a most im-
portant point as showing the manner in which variations have

affected the whole of embryonic development. As examples I may mention the small outer toes on the feet of the pig and probably of other Ungulates, the large digit of the ostrich's foot and of the kangaroo's foot, the spiracle of Elasmobranchii,[1] the rudimentary character of the phalanges of the bird's hand. I have no doubt that many other instances will occur to my reader. (3) Organs which have been recently acquired may appear at the very earliest possible stage; e. g. the double hallux present in some breeds of fowls makes its appearance as soon as the other digits; the webbing of the duck's foot is not preceded by a stage in which the digits are separate. In short, the evidence seems to indicate that in a great number of cases adult variations of any part are accompanied by precedent similar alteration of the same part in the embryo. I do not mean to affirm that the alteration of the organ in

[1] The spiracle of Elasmobranchii is a reduced gill-cleft, and in correspond-ence with its reduction in the adult it is found to be reduced also in all stages of its development from its very first appearance, which takes place after the hyobranchial cleft—not before it, as would be expected from its position as the anterior member of a series (see Self, " Notes on Elasmobranch Development," this Journal, vol. xxxiii, p. 572). It would be excessively interesting in this connection to ascertain whether any trace of the spiracle is present in the embryos of those Elasmobranchs in which it is absent in the adult. In fact, an account of the spiracular cleft throughout the Vertebrata is much needed. Is it present in embryo in Teleosteans and in Lepidosteus ? Balfour asserts that it is present in the former ('Comp. Embryology,' vol. ii, p. 77, mem. ed.), but I am unable to find his authority for the statement. He also states that it is present in the embryo Lepidosteus as a double layer of cells without a cavity (Balfour and Parker on 'Anatomy and Development of Lepidosteus,' mem. ed., pl. xxxvii, fig. 43), but, so far as I am aware, his interpretation of this structure has not been confirmed. In Amniota—through-out which the pharyngeal clefts present a very remarkable constancy—the spiracular cleft is as large, if not larger, than the succeeding one, and appears first in development. This is an exceedingly interesting fact, which has not been sufficiently noted. It tends to show that the Amniota have arisen from aquatic forms independently of the terrestrial Amphibia, in which group the spiracular cleft is not formed at all—though a slight rudiment of it does appear for a short period. In fact, we may take it as a fact of systematic value that the spiracular cleft is absent or rudimentary in all Ichthyopsida, while it is present in relatively normal development in all Amniota.

the embryonic stage[1] is the same as it is in the adult. It may be altered relatively more or it may be altered relatively less; the point is that it is altered in the same direction as the adult organ. And this is surely what we should expect when we remember that embryonic development is the preparation of the free form in the most perfect state and at the least expense. If this view is correct that variations are present in the embryo—that an organ which is enlarged, diminished, or suppressed in the adult is correspondingly, or nearly so, enlarged, diminished, or suppressed in the embryo,—then I ask, how are we to account for those cases which most undoubtedly occur in which records of previous states of structure are present in the embryonic history, e. g. the pharyngeal slits of Sauropsids, the tubular heart, the vascular arches, the embryonic kidney of the same group, and many such. The point is this: organs which have been recently altered show a similar alteration in the embryo, whereas some organs, like the gill-slits, which must have been altered very far back, do not show a corresponding embryonic alteration, but persist more or less in their old form without discharging the original functions or being of any use to the embryo. In other words, some ancestral organs persist in the embryo in a functionless rudimentary (vestigial) condition and at the same time without any reference to adult structures, while other ancestral organs have disappeared without leaving a trace. The latter arrange-

[1] It appears that in some cases, at least, it is less in the embryo. E. g. sternal ribs of ostrich are generally five in adult, rarely six; in embryo, they appear always to be six. In birds the fibula reaches the tarsus in embryos, but very rarely does so in adults.

A case of this kind which might be investigated is this :—In the golden plover the hallux is entirely absent, whereas in other plovers it is present. Has the golden plover any trace of it in the embryo?

I am aware that it is often held—Darwin held it—that rudimentary organs are, relatively to the adjoining parts, larger in the embryo than in the adult. But unless this fact can be shown to be universal, it has but little value because it applies to many other organs in the embryo which are not rudimentary, e. g. brain, eye, heart, and kidney. This difference in relative size is probably simply owing to the fact that the bulk of the skeletal, muscular, and connective tissues of the embryo is relatively less than in the adult.

ment seems to be the rule, the former the exception. How
are we to account for the exception ? The key to the position
is, in my opinion, to be found by comparing the conditions of
larval and embryonic development. In larvæ the organs are
functional and the animal is getting its own living during the
development, whereas in embryos the development takes place
under the protection of egg membranes, the pupal case, or the
uterine wall, and the organs are for the most part functionless,
special arrangements being made for the supply of nutriment.
These two developments have generally not been properly dis-
tinguished by naturalists writing on this subject.

In embryos the organs are for the most part functionless
and without relation to the maintenance of life; consequently
there is nothing to counteract the tendency to the appearance
of a variation at all stages in the life of an organ. In larvæ,
on the other hand, the organs are functional and the con-
ditions of life may be different from those of the adult. They
have to maintain themselves during the various phases of their
development; consequently if a variation of an organ at one
stage is injurious to the same organ at a previous or subsequent
stage, it will be eliminated at the stages at which it is injurious.
In this way, as will be readily seen, natural selection will com-
pel the limitation of variations in an organ to particular stages
in the development of that organ; the power of natural selec-
tion will inevitably prevent a variation useful at one stage
from affecting another stage of the same organ in which its
presence would be injurious to the larva. Thus there must be
in larvæ a tendency to the inheritance of variations at corre-
sponding periods, and to the elimination of them at other
periods when they would be harmful to the organism.
Thus it must happen that if variations occur which enable the
adult to change its condition of life, and if at the same time
the old habits of life are retained by the last larval stage, then
the old arrangement of organs will be retained by the larva.
In this way, as the adult form gradually progresses in evolution,
not only one but a whole series of larval stages might become
established, each one being based upon some ancestral stage of

structure and retaining some ancestral habit of life. But of
course these larval stages are liable to vary and are subject
to the natural selection engendered by the struggle for life.
So they may themselves become modified and the ancestral
habits and structure which they have inherited may also become
modified. It thus becomes apparent that larvæ will often retain
traces more or less complete of ancestral stages of structure,
and that they will do this in virtue of the operation of the
force of heredity and of natural selection. And the retention
of ancestral features by the larvæ will be the more complete the
more completely the ancestral habits of life are retained by
them. There is, then, in larvæ a tendency to the inheritance of
variations at corresponding periods, and in this respect larvæ
differ from embryos.

To sum up, I would maintain that ancestral stages of struc-
ture are only retained in so far as they are useful to the free-
growing organism, i.e. to the larva in its free development.
Or, to put the matter in another and more recondite form,
modifications appearing in and affecting the adult structures
will similarly affect the same structures all through the
development of the offspring unless the old structural arrange-
ments are called into being in the development of the offspring
by the application of the old stimulus, viz. the same external
conditions of life.

In embryos, on the other hand, the organs are for the most
part functionless, and there appears to be no reason for the
retention of ancestral conditions of structure. On the con-
trary, as I have shown above, most organs when modified in
the free-living state are similarly modified in the embryo.
And, as I have already insisted, this is what we should expect
when we remember that embryonic development is the pre-
paration of the free form in the most perfect state and at the
least expense. How is it, then, that we do get in embryos in
certain cases a most remarkable preservation of ancestral
organs and conditions of structure which have been lost in the
adult? I think it can be shown that the retention of ancestral
organs by the larvæ after they have been lost by the adult is

due to the absorption of a larval or immature free stage into embryonic life.

Let us take an example.   Let us try to picture to ourselves the steps by which the tadpole stages of the frog might be lost, so that the adult frog arose direct from the egg.   The larval organs of a tadpole cannot disappear one by one independently of one another.   If the gill slits disappeared before the heart had become double and the lungs had developed, the tadpole would die of asphyxia.   In order to completely obliterate the piscine stage from the tadpole, you require a number of nicely co-ordinated variations affecting different organs in very different ways—all tending to the atrophy of those organs which adapt it to an aquatic life and to the development of the organs required for terrestrial life. Such a combination of suitable variations as is here re-quired—such an inversion of the original evolutionary changes —is very unlikely to occur,[1] especially when the same object can be obtained, namely the obliteration of the piscine phase in the frog's life, by a simple single variation—that is to say, by the mother becoming viviparous and retaining its young within its uterus or oviduct until the piscine stage of develop-ment has been passed through; or by the ovarian ovum de-veloping a greater amount of yolk, so that the whole develop-ment up to the close of the piscine stage can take place before hatching at the expense of the yolk.   That larval stages do disappear and embryonic stages arise in this way is shown by the case of the viviparous salamander (Salamandra atra), in which the gills, &c., are all developed but never used, the animal being born without them.   Here, therefore, is an actual case in which the larval phase has disappeared by becoming embryonic and therefore functionless, and therefore largely removed from the direct action of natural selection; once em-

[1] It has been suggested to me here that this combination of variations must have taken place in phylogeny, otherwise the terrestrial animal could not have been evolved; why not then in the larva?   To this I reply: there is no necessity for the long and laboured changes to be gone over again in inverted order in the case of the tadpole, because the object can be obtained by the simple inclusion of the tadpole stage within the embryonic period.

bryonic only, the conditions of its existence are totally altered.
Its disappearance is no longer a matter of importance to the
organism, because the embryo being protected from the struggle
for existence the presence of rudimentary functionless organs
is unimportant to it. They therefore persist, and it is this
persistence which has given rise to von Baer's law. But von
Baer's law is imperfect, because it omits to take cognisance of
the fact that embryonic features are no more constant than are
the adult characters; that indeed they vary with the adult
characters, so that no adult character is changed without some
precedent alteration of all the previous embryonic phases. The
embryonic life is a connected whole, and it is impossible that
an isolated alteration of one particular stage can have taken
place. All variations must run through the whole develop-
ment; they may come out strongly at one particular stage, but
they must have been led up to and followed by variations in
all other stages.

Embryonic variations are not for the most part acted upon
by natural selection, because they concern rudimentary organs
only; but when free life is reached, and the organs become
functional, the same variations continued (for continue they
must) are put to the test, and the organism stands or falls by
them. The constancy of development in the same species
proves this point; for if the embryonic stage could vary without
the free stages being at all affected, then, as natural selection
does not act upon rudimentary embryonic organs, the em-
bryonic organs would run riot, and we should expect to find
the greatest diversity in embryonic development of the same
species, and this we do not find; and this applies not only to
organs which persist into the adult, but also to organs which
disappear before the adult stage is reached. These purely
embryonic structures must have some nexus with structures
which succeed them in development, and a variation in them
must be accompanied by variations in these later appearing
persistent organs. In fact, it seems to me most important to
remember that the various stages in the development of an
animal are just as much correlated as are the different organs

of the adult animal with one another.   I repeat, the constancy
of development in the same species proves this point, as do the
small but constant differences between the embryonic phases of
slightly different but distinct species.

Granting that embryonic rudiments do vary, of which I do
not think there can be any doubt, then it would appear that
the variations must be selected, not with regard to their
intrinsic[1] merits at the moment as is the case with variations
in functional organs, but with regard to the effect of their de-
scendent or correlated variations in the adult.   So it comes
about that the embryonic rudiments in one group of animals,
though resembling generally those of another group of the
same class or phylum (just as the functional adult organs
resemble one another generally), yet differ from them in minor
points, so that the group has its own individual character with
regard to that particular rudimentary organ, just as it has its
own individual character with regard to any adult functional
organ.

The conclusion here reached is that, whereas larval develop-
ment must retain traces (it may be very faint) of ancestral
stages of structure because they are built out of ancestral
stages, embryonic development need not necessarily do so,
and very often does not; that embryonic development, in so far
as it is a record at all, is a record of structural features of pre-
vious larval stages.   Characters which disappear during free
life disappear also in the embryo, but characters which though
lost by the adult are retained in the larva may ultimately be
absorbed into the embryonic phase and leave their traces in
embryonic development.

[Throughout the above discussion I have, to avoid complica-
tion, treated all embryonic organs to be functionless; but it

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[1] By intrinsic merits at the moment, I mean the effect on the organism as a
whole at any particular moment.   A variation in a rudimentary functionless
organ of an embryo can have no effect upon the welfare of the embryo
(excluding secondary effects—if any—of interfering with functional organs,
e. g. blood-vessels); its utility can only be judged when the free state is
reached.

must not be forgotten that some of them are functional and
that these resemble organs of larvæ in retaining ancestral
features, e. g. the ductus arteriosus, &c.]

To put the matter in another and more general way, the only
functionless ancestral structures which are preserved in develop-
ment are those which at some time or another have been of
use to the organism during its development after they have
ceased to be so in the adult. In this way I should be inclined
to explain the hair of the human fœtus and the teeth of the
fœtal whale—that is to say, I should be inclined to suppose that
the possession of the lanugo is due to the fact that there was a
time in the evolution of man when the babe required this
protection against the cold after the necessity for it had dis-
appeared in the adult, and that the young whale in the days
when whalebone was first acquired still retained the ancestral
habits which required teeth. It is, however, possible that
these and other similar cases of the retention of rudimentary
organs in late embryonic life have another explanation, and_it
becomes necessary to collect and examine as many cases as
possible of the undoubted retention, as embryonic rudiments, of
organs which we have reason to know have recently disappeared
from the adult stage.

The retention of such organs in the embryo may, as I have
hinted, be due to the fact that they have been retained func-
tionally by the young animal after they have been lost by the
adult; but another explanation is possible, which is that
organs which are becoming functionless, and disappearing at
all stages, may in some cases disappear unevenly; that is to
say, they may remain at one stage after they have totally dis-
appeared at another. In this manner we might get an organ
which had become quite functionless and had quite disap-
peared in the free stage, still persisting, though with a much
reduced development, in the embryo. It is possible that the
lanugo and the teeth of fœtal whales may be explicable in this
manner. But that such a retention of organs in the embryo
is not an important or permanent one is shown by the fact of
their comparative scarcity in embryonic histories. This is a

most important subject, and I propose in a future paper to collect and examine as many cases as I can find of the retention in the embryo of organs which have lately disappeared in the adult.

There is another aspect of the same question which is suggested by the above considerations, viz. if an organ can disappear unevenly there is no reason in the nature of things, so far as I can see, why it should not disappear in its developing embryonic stages before it does so in the adult, so that there would still be found in the adult a persistent useless rudiment of it after all trace had gone in the embryo. And we may even go further than this, and maintain that if organs can disappear unevenly it is conceivable that traces of an ancient organ might appear and disappear more than once in the course of development. Of the last-suggested phenomenon I know of more than one instance, but I know of no instance of an organ disappearing in its embryonic stages while still persisting as a rudiment in the adult. As an example of the repeated appearance and disappearance of a rudimentary organ in embryonic development I may mention the neurenteric canal of certain species of birds as described by Gasser,[1] and quoted by Balfour in the 'Comparative Embryology' (vol. ii, p. 162, mem. ed.). The anterior neuropore of Ascidians, which appears twice in the development, is another example of the same phenomenon. Although I know of no instance of an organ disappearing in the embryo before it totally disappears in the adult, I do know of instances of rudimentary embryonic organs which have disappeared in their earlier stages while still present at a later stage, e. g. the muscle-plate cœlom of Aves, the primitive streak of Amniote blastoderms, and the neurenteric canal of Aves; and I have no doubt that many instances of this might be collected.

From the application of the principles set forth in the preceding pages it becomes apparent to us why it is that in the

[1] Gasser, "Der Primitivstreifen bei Vogelembryonen," 'Schriften d. Gesell. zur Beförd. d. gesammten naturwiss.,' zu Marburg, vol. ii, sup. 1, 1879.

higher animals it is the early stages of development which have the greatest interest for us, the later stage having been added at a time when, as now, the immature stages of free life were but little marked, and consequently there was but little chance of the incorporation of any ancestral features in the embryonic development. It also helps us, I think, to understand why the most interesting of the ancestral embryonic features were related to the passage from the aquatic to the terrestrial condition, because when this took place in phylogeny there must have been a most pronounced aquatic larval stage, such as we find to-day in Amphibia.

APPENDIX.

Mr. J. J. Lister has pointed out to me as confirmatory of the views set forth in the preceding pages that there is at least one exception to the rule that animals produced by budding show no ancestral rudiments in their development, viz. the sexually mature medusoid spore-sacs. These organisms present in their development traces, as is well known, of many organs which they must formerly have possessed in a functional condition, e. g. the umbrella cavity, the marginal tentacles, the circular canal, &c.; but, as Mr. Lister points out, these spore-sacs differ from other buds in this important fact that they have most undoubtedly had quite recently a free life during the maturation of the generative products; and it may be that it is the impress of this ancestral free life which has given rise to the ancestral features in the development.

On the Inadequacy of the Cell Theory, and on the Early Development of Nerves, particularly of the Third Nerve and of the Sympathetic in Elasmobranchii.

By

Adam Sedgwick, F.R.S.

IT is now more than ten years ago since I first pointed out the inadequacy of the cell theory. That I did so in a very guarded manner need hardly be said; but now, after ten years of mature work, I feel justified in giving a stronger expression to the views which I then formed, and which all my subsequent work has amply confirmed. My words then (in 1883) were as follows :—"In short, if these facts are generally applicable, embryonic development can no longer be looked upon as being essentially the formation by fission of a number of units from a single primitive unit, and the co-ordination and modification of these units into a harmonious whole. But it must rather be regarded as a multiplication of nuclei and a specialisation of tracts and vacuoles in a continuous mass of vacuolated protoplasm." Again, in 1888, in the preface to my "Monograph on the Development of the Cape Species of Peripatus,"[1] I wrote: "It would appear, indeed, that in Peripatus the cells of the adult, in so far as they are distinct and sharply marked off structures, are not, as appears to be generally the case, present in the earliest embryonic stages, but are gradually evolved as development proceeds. In other words, the cell-theory, if it

[1] 'Studies from the Morphological Laboratory of the University of Cambridge,' vol. iv, part 1.

implies that the adult cells are derived from embryonic cells which have been directly produced by the division of the ovicell, does not apply to the embryos of Peripatus."

In the days when these words were written it was a general belief among leading histologists and physiologists that the connections which were known to exist in some cases between adult cells had arisen secondarily, and that the primary condition brought about by the cleavage of the ovum was a complete separation from one another of these units, of which the body was supposed to be composed. There has been, no doubt, a change of opinion since those days, and although many biologists would still maintain that cleavage is complete and results in the formation of separate units which later become connected, there is a constantly increasing number who would consider themselves misrepresented if one imputed to them this belief not long ago universal, and the belief which was supposed to follow from it, that the first stage in the evolution of the Metazoa was a colonial Protozoon. But, as I have said, opinions have changed since those days, and I quote my words, written then, to show that I have long held the view which I am now expressing, and that I was among the first to attack a theory which had even then passed its stage of usefulness, and is now holding men's minds in an iron bondage. For although opinions have changed on this important subject, and although there are some who think that they have escaped from the domination of this fetish of their predecessors, yet as a matter of fact the cell theory is still rampant, still blinds men's eyes to the most patent facts, and still obstructs the way of real progress in the knowledge of structure.

In order that I may not be met with the statement that such a state of things exists only in my own imagination, that I am putting up a dummy merely to knock it down again, it is necessary that I should give some proof that this hypothesis has still the power which I ascribe to it. What is the cell theory? I am not concerned with what its authors held; what we want to know is, what is the present form and

extent of it ? What is the point of view which it compels its votaries to take ?

It is not easy to answer this question ; it is, in fact, as difficult to answer as that other question so often asked of the teacher by his pupil—what is a cell ? The source of the difficulty is that we are dealing with a kind of phantom which takes different forms in different men's eyes. There is a want of precision about the cell-phantom, as there is also about the layer-phantom, which makes it very difficult to lay either of them. Neither of these theories can be stated in so many words in a manner satisfactory to every one. The result is that it is not easy to bring either of them to book.

To answer the question—what is the cell theory ?—the best plan will be to consider for a moment the ideas which are taught to the student of biology, and which influence him in his future work. We tell him that the cell is the unit of structure, that an organism may consist of a single cell, or of several cells in association with one another: we draw the most fundamental distinction between the two kinds of organism, and we divide the animal kingdom into two great groups to receive them. As a proof of the importance which we attach to this feature of organisation we assert that a man is nearer, morphologically, to a tapeworm, than a tapeworm is to a paramœcium. We tell him that the various structures present in a protozoon are all parts of one cell, whereas in a metazoon the various parts are composed of groups of cells which differ from one another in structure. Finally, when we ask him in the examination to tell us the principal differences between hydra and vorticella, we consider that he is very inadequately prepared if he does not sum them up by saying that hydra has tissues composed of definite cells and is multicellular, while vorticella is without definite cellular tissues and is unicellular. Carrying on the idea thus implanted in his mind as to the fundamental importance of the cell, we tell him about the neuro-epithelial cell and the myo-epithelial cell, and we point out their primitive distinctness,—an idea which is still further impressed upon him when he studies the

connection between nerve and striated muscular fibre. Finally,
when he comes to study embryology, the importance and dis-
tinctness of the cell meets him at every step, from the complete
cleavage which he is led to believe is primitive, to the develop-
ment of nerves according to the views of His.

So much for the student in the schools : now for the investi-
gator in the laboratory. He studies the ovum and maintains
its absolute isolation in the organism ; or he examines epithelial
cells and draws them as isolated structures separated by sharp
boundary lines ; or he labours to prove the continuity between
the nerve and muscle, or between the nerve and secreting cell :
so much is he dominated by the idea of separate cells that he
considers that the burden of proof rests rather with the man
who asserts such continuity than with him who denies it.
Or, if he be an embryologist, he will talk of, and figure, the
proliferation of cells at the primitive streak ; he will describe
the nascent ganglion cell sending a process from the developing
spinal cord into the anterior root, and he will figure it ; he
will talk of mesenchyme cells, and figure them for the most
part separate from one another.

I take it that this is a not unfair account of the training a
zoologist receives at the present day, so far as the cell is con-
cerned, and of the ideas which dominate him in his later work.
He believes that the cell is the unit of structure, and that it
forms the basis of organisation in the Metazoa; it is the func-
tions of the cell and the relations which it enters into with
other cells which forms an important subject of current biolo-
gical investigation. Who, then, can deny that the cell theory
is still a living power in the school of biology ? That it blinds
men's eyes to the most patent facts, and obstructs the way of
real progress in the knowledge of structure, it will now be my
endeavour to show. For this purpose I shall deal on this
occasion with the origin and structure of two tissues of the
Vertebrate embryo—the so-called mesenchyme and the system
of peripheral nerve-trunks. My results are the product of many
years' work, and will, I hope, be published in greater detail and
with figures on a future occasion.

The So-called Mesenchyme Tissue of Elasmobranch Embryos.

This tissue is always described as consisting of branched cells lying between the ectoderm and the endoderm. The cells are spoken of as being separate from one another, and from the adjacent ectoderm and endoderm, excepting at points where they are supposed to arise from one of the primary layers. And not only are they described as being separate cells, but they are actually drawn in the author's figures as separate from each other. This is, perhaps, the best instance that can be given of the bondage in which the cellular theory holds its votaries. For what are the facts? The separate cells have no existence at all! In their place we find, on looking into the matter, a reticulum of a pale non-staining substance holding nuclei at its nodes. It is these nodes, with their nuclei, which are drawn by authors as the separate branched cells of the mesenchyme, and they are constrained by this theory, with which their minds are saturated, not only to see things which do not exist, but actually to figure them. Another erroneous view due to the same cause is the view that this mesenchyme tissue is not continuous with the ectoderm or with the endoderm; whereas, as a matter of fact, the opposite is the case, for the primary layers are simply parts of this reticulum in which the meshes are closer and the nuclei more numerous and arranged in layers. These are facts of which anyone with an unbiassed mind can convince himself by the simple inspection of a Selachian or an Avian embryo, and they would have been recognised long ago had it not been for the dominating influence of the cell theory.

The current views as to the origin of this tissue show just as conspicuously the influence of the same theory. It is said to arise by the budding-off and migration of cells from the walls of the embryonic coelom, from the primitive streak, and from the neural crest; and the space between the ectoderm and endoderm into which these cells migrate is described as being empty of structural elements. What are the facts? The

space between the layers is never empty; it is always traversed by strands of a pale tissue connecting the various layers, and the growth which does take place at the places mentioned is not a formation of cells, but of nuclei which move away from their place of origin and take up their position in this pale and at first sparse reticulum which exists between the layers. As this reticulum, which has always existed, becomes infested with nuclei it increases in bulk, and forms the conspicuous reticulate tissue which is by some authors called mesenchyme. The primitive streak, the walls of the coelom, and the neural crest, and, as Goronowitsch[1] has shown, parts of the ectoderm, are growing points where nuclei, not cells, are produced. These facts I described long ago in the development of Peripatus, and it is the recognition of the same processes taking place in the Vertebrata in an even more conspicuous manner that has induced me to again call attention to their importance.[2]

The Origin of Nerve-trunks and the Fate of the Neural Crest.

If there is one point more than another on which the cell theory has led anatomists completely astray, it is upon this one. We may take it that the new views upon the origin of the peripheral nerves began with Balfour's discovery of the structure which is generally called the nerve crest. Before that discovery nerves were supposed to develop in situ in the mesoderm; after it, there were two principal views as to the origin and growth of nerves: one of these was that cells of the central organ grew outwards as strings to the periphery; while, according to the other, nerve-fibres are the elongated pro-

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[1] 'Morpholog. Jahrb.,' Bd. xx, 1893.

[2] At the same time Peripatus shows certain features more clearly than the Vertebrate; I would refer especially to figs. 24 *d* and 26 *d* on pl. v of my Monograph, in which, while the so-called ectoderm and endoderm are obviously parts of the same layer, or tissue : they are separated by a region in which the vacuoles are larger, the protoplasmic strands less numerous, and nuclei are conspicuous by their scarcity.

cesses of cells either of the central organ or of the ganglia.
Both these views are erroneous; and if both were not inspired
by the cell theory, they were both promulgated at a time when
that theory was at its zenith. The earlier view, that nerves
were developed in situ from the mesoderm, was much nearer
the truth.

The nerve crest does not, as was first stated by Balfour and
afterwards by all authors on the development of nerves, give
rise exclusively, or even principally, to nerves and ganglia. It
gives rise to nuclei which spread out in, and add to the meso-
blastic reticulum, which at all times, i.e. from the very begin-
ning, exists between the layers, and to nuclei which become
the nuclei of the rudiments of nerve ganglia. The nerves are
developments of the reticulum; they are elongated strands of
the pale substance composing the reticulum, with some of its
nuclei; and their free ends branch out into the fibres of the
reticulum, and are added to by the latter falling into the line
of the growing nerve. Neither they nor the ganglia appear
until the nerve crest is breaking up. The reticulum further
gives rise certainly to smooth muscular fibres, connective
tissues, and blood-vessels, and probably also to striated
muscle. It is also continuous with all the so-called epithelial
tissues of the embryo; indeed this latter substance is to
be regarded as consisting only of one or more layers
of nuclei embedded in the outer part of the reticulum,
which is rather denser than elsewhere in correspond-
ence with the greater density of the nuclei. Nerves
are a gathering up, so to speak, of the strands of the reticulum
into bundles, and are formed in that way; or, to put the matter
in another way, nerves are a special development of the reti-
culum along certain lines. These special developments are
generally marked by an increase in the number of nuclei, such
increase being particularly great in the neighbourhood of the
ganglia.

To sum up the matter, the nervous and muscular tissues are,
as they were in Peripatus (see my Monograph, p. 131),
special developments of the same primitive reticulum, a com-

munity of origin which renders their adult relations perfectly
intelligible.   Further, I have no hesitation in saying that His'
descriptions of the development of nerve-fibres as processes of
central or ganglionic nerve-cells, does not apply to Selachians;
inasmuch as nerves are laid down long before any
trace of nerve-cells can be made out.   The neuroblasts
of His and of other authors are nuclei lying in a substance
which, after death caused by the ordinary reagents, has usually
a fibrous structure.   This substance is continuous with, and
therefore a part of, the reticulum outside.   The cell-processes
which have been described as growing out from the neuroblasts
are merely parts of this reticular substance, the fibres of which
become arranged more or less in the direction of the long axis
of the nuclei, and the meshes correspondingly drawn out and
narrowed.   Many of His' drawings even show that this is so,
and an inspection of the specimens leaves no doubt at all about
the matter.   In short, the development of nerves is not
an outgrowth of cell-processes from certain central
cells, but is a differentiation of a substance which
was already in position; and this differentiation
seems to take place from the medullary walls out-
wards to the periphery, both in the anterior and
posterior roots, and to precede, or to proceed pari
passu with, the development of other tissues.   The
nerve crest is, then, to be regarded as a centre for the growth
of nuclei, which spread into the body of the embryo and be-
come concerned in the formation of many tissues, nervous
tissues amongst the rest.   There are many other such centres
for the production of nuclei; for instance, I may mention the
walls of the cœlom, the caudal swellings, and in the Amniota
the primitive streak.   All these centres of growth are in
so-called epithelial tissues.   This is, of course, necessi-
tated by the fact that Selachian embryos are at one stage
composed entirely—or almost entirely—of these so-
called epithelial tissues; as are many embryos, e. g. those
of Peripatus and of Amphioxus.[1]   These facts will be dis-

[1] The significance of this epithelial structure of the young embryo—this

puted by many morphologists, but they are easy of proof by
the simple inspection of good preparations to minds not warped
by the cellular theory as ordinarily taught. In fact, had it not
been for the undue persistence of this hypothesis beyond the
time of its fruitful life, they would have been recognised long
ago, and much needless waste of labour in trying to make the
facts of nerve-development conform to the theory would have
been saved.

The nerve-crest in Selachians (Scyllium, Acanthias,
Raia, and Pristiurus) is, as I pointed out some time ago
("Notes on Elasmobranch Development," 'Quart. Journ. of
Micr. Sci.,' vol. xxxiii), from its first appearance, in three
pieces.[1] The first of these pieces reaches from the region of
the fore-brain to the hind brain. The posterior limit of it is
marked in older embryos by the root of the trigeminal nerve.
It gives rise to the reticulum of the front part of the head,
and contributes to that of the mandibular arch. The
following nerves are formed within its limits :—The trigeminal
and its branches, which include the so-called ramus ophthal-
micus profundus with the ciliary ganglion and the third
nerve (see below). Very possibly other nerves, viz. the
fourth, the sixth, and the olfactory, may be also developed
from this part of the reticulum, but I have no observations on
this point.

The manner in which these nerves are laid down may be
described as follows :—When the nerve-crest, which in this
region of the head very early spreads ventralwards on each
side of the brain, is breaking up into the reticulum, certain
tracts of it remain unaltered and characterised by a greater
density of nuclei. These tracts mark the course of the future
nerves and the sites of the future ganglia. They them-

collection of the nuclei at the surfaces, as it may be described—I hope to con-
sider in another place. Now, I may merely hint that it is probably due to the
impress of some well-marked larval phase in earlier stages of evolution (see my
article on "von Baer's Law, &c.," in 'Quart. Journ. Micr. Sci.,' vol. xxxvi).

[1] Goronowitsch ('Morph. Jahrb.,' Bd. xx) has recently found the same fact
for the bird, but he makes no reference to my results on this point.

selves continue to break up, but a kind of core remains
which constitutes the foundation of the future nerve and
ganglion. The Gasserian ganglion, the ophthalmicus pro-
fundus, the mandibular branch of the fifth, and the ciliary
ganglion thus gradually emerge from the remains of the nerve-
crest—are, so to speak, crystallised out of it. At first they
have the form of dense cords of nuclei; but they soon acquire
some of the non-staining fibrous substance, which makes its
appearance as a rule in their central portions, so that for a
time sections of these nerves exactly resemble in appearance
sections of the nerves of Invertebrata, e. g. Peripatus,
Chiton, &c. This description holds for an embryo of 85 mm.,
beyond which stage I have no observations. The nuclei which
have peeled off, leaving the nerve-trunk below, give rise to the
muscular and connective tissues of the parts concerned, the
reticulum of which is freely continuous with that of the nascent
nerve, especially at the free end of the latter. It thus be-
comes apparent that these tissues—nervous, muscular,
connective, and vascular—are all developed in continuity.[1]

While the Gasserian ganglion, the mandibular branch of the
fifth, the ophthalmicus profundus, and the ciliary ganglion all
crystallise out of the nerve crest; the third nerve does not do
so. It arises as a differentiation of the reticulum formed by
the breaking up of the nerve crest, and it first makes its
appearance as a forward projection of nuclei from the ciliary
ganglion. This, by a gradual differentiation of the reticulum,
extends itself until it reaches the base of the mid-brain, with
which it becomes continuous by means of an increase in the
pale fibrous strands which pass between the medullary wall
and the reticulum. The third nerve is at first a cord of nuclei
and rather dense pale substance. The third nerve,[2] there-

[1] The continuity of the embryonic tissue which will give rise to the
nervous and muscular tissues is well seen in the embryo of Peripatus
capensis, and I have already hinted at this fact in my Monograph on the
development of that species at pp. 131 and 133, and figured the tissue as
nerve musc., pl. x, fig. 5.

[2] It will be evident, if my observations are correct, that I have found an
earlier stage of the third nerve than Dohrn describes in his sixteenth study. In

fore, presents this interesting and remarkable pecu-
liarity in Scyllium and Acanthias; it grows or is
differentiated from the ciliary ganglion to the floor
of the mid-brain, and not in the opposite direction, as has
hitherto been supposed. The proof of this is to be found in the
fact that in a Scyllium and Acanthias embryo of 9 to
11 mm. the third nerve can be seen projecting forwards from
the ciliary ganglion, and ending in front in the reticulum,
short of the floor of the mid-brain. The ciliary or profundus
ganglion is at one time—when it is first laid down—in contact
with the ectoderm. Later it is shifted inwards, but remains
connected for a time with the ectoderm by a cord of cells,
which eventually disappears. This point has been seen by
van Wijhe.

The embryonic medullary wall[1] is connected with the
reticulum by pale fibres similar to those which compose
the reticulum, and the nerve-roots, both anterior,
posterior, and cranial, are special enlargements of
such connecting strands. They are formed at a time
when no structures which could be called cells by any but a
fanatical devotee of the cellular theory are present, either in the
medullary wall or in the ganglionic rudiments; and in a manner
which, if closely followed, renders it quite impossible to speak
of growths one way or the other, excepting that one can make
one assertion, viz. the pale fibrous substance which marks the
nerve appears both in the anterior and posterior roots, and in
the cranial nerve-roots next the central organ, at a time
when the white matter (which is composed of this pale
fibrous substance) first appears as a thin layer, and in
continuity with such white matter. The differentiation
outwards proceeds from this point, and the nerve-
rudiment always ends by branching out into the fibres

my fuller paper dealing with this subject I hope to examine Dohrn's results in
detail.

[1] Inasmuch as the nerve-crest is derived from the medullary wall and gives
rise to mesodermal structures, the medullary wall itself gives rise, in part, to
mesoderm.

of the reticulum. The only exception to this rule is the
third nerve of Scyllium and Acanthias (and probably
others), which is undoubtedly differentiated from the ciliary
ganglion to the floor of the mid-brain; but this is, perhaps,
more an apparent exception than a real one, because the
ciliary ganglion belongs to the fifth nerve and the order of
fibrous differentiation is normal, viz. from the root of the fifth
nerve, through the ciliary ganglion, to the floor of the mid-
brain.   I commend this observation on the development of the
third nerve to the physiologist, with a view to a renewed
investigation of its functions.   It is rendered the more inter-
esting by the fact that in Lepidosiren it is commonly stated
that the area of the third nerve is supplied by the ophthalmic
branch of the fifth, the third nerve being absent.[1]

I have already, in my 'Notes on Elasmobranch Develop-
ment,' stated my reasons for believing that the views put
forward by Hensen as to the origin of nerves were nearer the
truth than those of any other zoologist.   I have, in this paper,
shown not only that the network required does exist, but also
how it arises, and how it gives rise to the rudiments of the
peripheral nerve-fibres.   Minot, in his 'Human Embryology,'
p. 624, says that Hensen's theory of the origin of nerves
"cannot be adopted because the outgrowths of the nerve-fibres
have been observed; moreover, Altmann has pointed out that
the fibres seen in the embryonic mesoderm are really pro-
cesses of the mesoderm cells, and, as shown in the excellent
fig. 2 of his plate, are quite distinct both from the ecto-
derm and endoderm." (The italics are mine.)   This passage
is, according to my work, full of errors; for I maintain, as
the result of long and careful observation, extending over
many years, that the outgrowth of nerve-fibres from cells in
the ganglia and medullary wall not only has not, but cannot

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[1] This statement rests on Hyrtl's work.   It must, however, be remembered
that his specimen was confessedly rotten in its nervous tissues, and by the
fact that v. Wijhe ('Nied. Arch. f. Zoologie,' Bd. v, 1882) has found the
third nerve in Ceratodus.   Parker does not deal with the brain and nerves
in his memoir on Protopterus.

be observed; that the fibres in the embryonic mesoderm are
not processes of mesoderm cells (as they are always figured),
which have no existence, but are parts of the reticulum which
has always existed from before cleavage onwards, connecting
together the various parts of the developing ovum; and that
this reticulum is not separate from ectoderm and endoderm,
but freely continuous with both, they being but parts of it.
The almost universal practice of drawing this reticulum as
composed of separate branched cells is a most remarkable
instance of the manner in which a theory can blind men's eyes
to the most obvious facts.

Before concluding this general account of my work, I may
mention one or two other points of general interest which I
have noticed. Firstly, I may mention that in Scyllium there
are a number of anterior roots next the head, varying in
number from three to five, according to the age of the embryo,
without posterior roots. They no doubt give rise, as has been
suggested by others, to the so-called anterior roots of the
vagus. Secondly, Balfour was quite correct in the account he
gave of the origin of the sympathetic ganglia in Elasmobranchs.[1]
The ganglia arise as swellings on the posterior roots of the
spinal nerves, and soon become removed from the latter, so as
to form isolated masses connected with the spinal nerves by a
cord. These masses eventually become united longitudinally
into a chain. I may add to Balfour's account this fact, viz.
that no sympathetic ganglia are found within the area of
extension of the vagus ganglion. Or, if I am not correct in
applying the term " vagus ganglion " to the posterior part of
the vagus—the part which lies dorsal to the gill-slits and gives
off the branchial nerves—it would be better to say that sym-
pathetic ganglia are not found in the region of the branchial
slits, but begin immediately behind these structures. Thus,
in an embryo of 22 mm. the vagus ganglion and branchial

[1] I have not examined mammals on this point, but I think Paterson's
memoir ('Phil. Trans.,' 181) does not carry conviction. On the contrary,
there is, I think, in it internal evidence which inclines me to the view that he
has not got to the bottom of the matter.

region of the fore-gut ends at the level of the fifth anterior
root, and the first posterior root and the first sympathetic
ganglion occur at the level of the sixth anterior root. In
older embryos, in which the branchial region extends much
further back and overlaps a number of fully-formed spinal
nerves, the original sympathetic ganglia which were formed in
connection with the ganglia of these spinal nerves thus over-
lapped are found to have disappeared. The first sympa-
thetic ganglion appears always to be just behind
the branchial region, as in the adult, and sympa-
thetic ganglia are formed in Scyllium in connec-
tion with nerves which are without a posterior root.

Gaskell reproaches v. Wijhe with not knowing the true
meaning of a sympathetic ganglion, and one is tempted to ask,
does Gaskell himself know much more about it, or throw any
light upon the question? He says ('Journal of Physiology,'
vol. x, p. 162) that a sympathetic ganglion is the ganglion of
the anterior root of a spinal nerve which has travelled to a
variable distance from the central nervous system. As Dohrn
(seventeenth study, 'Naples Mit.,' Bd. x) very properly in-
sists, this view is at variance with the known developmental
history of the ganglion—which I am able to confirm so far as
its nuclei are concerned, and with the reservations necessitated
by the views set forth in this paper—and I am now able to
state that it is at variance with the fact that sympathetic
ganglia are entirely absent from those spinal nerves in which
the posterior root fails to reach its full development. In fact
one may say of these ganglia that they are always absent when
the posterior roots are not developed.

With regard to the fate of the neural crest described in this
paper, I should mention that I strongly hinted that it gave rise
to nuclei which entered the reticulum in my 'Notes on Elas-
mobranch Development,' p. 581, published in 1892; and that
Goronowitsch arrived independently at the conclusion that it
broke up into mesenchyme in the bird, and published his
results at some length in 1893 ('Morph. Jahrbuch,' Bd. xx);
but Goronowitsch failed to recognise the reticulum, and he was

unable to appreciate the full significance of the facts he described in their bearing on the question of the origin of nerves. Platt approximated to the truth with regard to the third nerve in her account of it as growing from the ciliary ganglion to the brain, but retained the error of her predecessors in regarding it as a cellular object, and not as a differentiation of the reticulum.

Minot has a characteristic comment on Platt's statement. He says ('Human Embryology,' p. 639), "This view rests probably on erroneous interpretation of observation, for it cannot be admitted that a motor nerve is formed by ganglionic fibres"! (The italics are mine, as is also the note of admiration.)

Contributions to the Life-History of the Foraminifera.

By

J. J. Lister, M.A.

WITH PLATES V.—VIII.

INTRODUCTION.

IN the preface to his classical work, 'Über den Organismus der Polythalamien,' published in 1854, MAX SCHULTZE acknowledged with regret the incompleteness of the account which he was able to give of the reproductive processes of the Foraminifera, and pointed out that a rich field here lay open for future investigation.

In the years that followed SCHULTZE himself made further contributions to our knowledge on this head, but, important as they were, they only went a short way towards solving the problem.

Of late MUNIER-CHALMAS and SCHLUMBERGER have contributed an essential factor in demonstrating the existence of dimorphism in many and widely separated species of Foraminifera. It has been shown in many cases that the individuals of a species fall into two distinct sets. In one, the first formed chamber is very minute, while in the other it is large. Differences in the size attained by the adult shell, in the plan of symmetry on which the chambers are arranged, and, as I have to show, in the nuclei may also be present. MUNIER-CHALMAS and SCHLUMBERGER distinguish the two groups as Form A, with a *megasphere*, and Form B, with a *microsphere*. I have ventured to modify one of these terms, and refer to the forms as

megalospheric (with a large central chamber), and *microspheric* (with a small central chamber) respectively.

What is the relation existing between these two forms of a species? Do they represent two sexes, or do they belong to different generations? I believe them to belong to different generations.

In what follows I have attempted to collect the more important evidence which bears on the life-history, and have given an account of my own observations, which deal mainly with two species:—*Polystomella crispa* (LINN.), belonging to the *Perforate* division of the group, and *Orbitolites complanata*, LAMK., a representative of the *Imperforata*.

The evidence will be presented under the following heads:—

    1.   Previous contributions to the life-history of the Foraminifera.

        a.   Observations on Reproduction and Dimorphism.
        b.   The relation of *Orbulina* and *Globigerina*.
        c.   Observations on Nuclei.

    2.   Observations on :—

        a.   *Polystomella crispa* (LINN.).
        b.   *Orbitolites complanata*, LAMK.
        c.   *Rotalia beccarii* (LINN.).
        d.   *Truncatulina*, D'ORB.
        e.   *Calcarina hispida*, BRADY.
        f.   *Cycloclypeus Carpenteri*, BRADY.

    3.   Concluding Remarks.

1. Previous Contributions to the Life-History of the Foraminifera.

(a.) *Observations on Reproduction and Dimorphism.*

In the year 1847, GERVAIS (12) brought before the Académie des Sciences, an observation on some Triloculine *Miliolidæ*, which he had kept in sea water. Young individuals, consisting of a single large chamber, with their shells already formed and capable of sending out pseudopodia had appeared, in number about 100, grouped about the orifice of a parent shell. He also states that

prior to the production of the young, individuals presenting differences in the form and size of shell, had come together in pairs on the side of the vessel. These individuals, he suggests, were male and female.

In 1854, MAX SCHULTZE published his work 'Über den Organismus der Polythalamien' (38). In it he described and figured young individuals of Miliolidæ and Rotalidæ. Examples of young Miliolidæ, consisting only of a spherical central chamber and tubular second chamber, are figured, and others in various stages of growth. He was struck by the marked difference in size of the central chamber presented by examples of the former group. From the figures it appears that the long diameter of the central chamber was in some cases 170 μ, and in others 35 μ. As will be shown below, these figures correspond approximately with the diameters of the central chambers in the megalospheric and microspheric forms of *Biloculina depressa*, D'ORB., one of the Miliolidæ (woodcut, p. 114). SCHULTZE, however, did not recognize the existence of dimorphism, and referred the individuals to different species.

In 1856, SCHULTZE made a further contribution (39) to the life-history of the Foraminifera. On May 15th, an example of the genus *Triloculina* which had been kept in sea-water, after remaining stationary on the wall of the vessel from 8 to 14 days, produced some 40 young. They were composed of colourless protoplasm contained in a shell consisting of a central chamber, having a diameter of 54 μ, and a tubular second chamber coiled about it. These gradually crawled away over the glass by means of pseudopodia. On breaking open the chambers of the parent shell, only a little granular material was found, and SCHULTZE concludes that all or nearly all the contents had been fashioned into the young. It is stated that the parent of the young Triloculinas was conspicuous by its larger size, among the other examples present.

In the same paper SCHULTZE described a form with a siliceous shell, which he provisionally called *Nonionina silicea*, in which numbers of spheres with siliceous coats, having a diameter of about 97 μ, were present in the chambers. The

evidence, as to the nature of these bodies which he took for the young, appears however to be less convincing.

In 1860, M. SCHULTZE described (40) the production of young in a species of *Rotalina*, closely allied to *R. nitida*, WILLIAMSON, which had been kept for about a year-and-a-half in an aquarium. The young consisted of three chambers of which the first was the largest, measuring 25–34 μ. He states that the central chamber of the parent shell was of the same size as that of the young.

In 1861, STRETHILL WRIGHT (45) recorded his observation of two large specimens of *Spirillina vivipara*, EHRB., surrounded by multitudes of very small ones; and within one of the large ones three small living *Spirillinœ* existed. EHRENBERG (11) had previously described and figured a specimen of this species containing two young shells near the mouth. In his figure, the central part of the coil of the young is represented of the same size as that of the parent. In the same paper, WRIGHT described a specimen of *Gromia*, partly filled with a "milky matter," which was found to consist of "large active molecules, like spermatozoa, in which there was no mistaking the characteristic movement."

In the same year, CARTER (10) called attention to the existence of spherules in the shells of fossil Foraminifera belonging to the following forms: *Nummulites*, *Orbitoides*, *Orbitolites mantelli*, *Orbitolina lenticularis*, and *Alveolina elliptica*. He considered that there could be "no reasonable doubt" that they were "propagative agents."

In 1865, SEMPER (43) sent home a short notice of a specimen collected on the reefs of the Pelew Islands, and referred by him to the genus *Nummulites*. As BÜTSCHLI points out ((6), p. 141), and as SEMPER's figures clearly show, the specimen was not a Nummulite, but one of the simple forms of the genus *Orbitolites*. The peripheral chambers are described as larger than those in the interior of the disc, and each contained a young individual invested by a shell, and consisting of a central chamber, and a second chamber surrounding it.

In 1875, SCHLUMBERGER (32) described two specimens of

12—2

the shells of *Miliolidæ* containing young ones. In one several chambers contained young shells, consisting of a nearly spherical chamber and a canal-like second chamber. In the second specimen two young ones, similar to those contained in the other specimen, lay in the terminal chamber.

In 1878, SCHNEIDER (37) described reproductive processes of different kinds in the genus *Miliola*.

In one species he found the protoplasm broken up within the shell into bodies of two sizes, of which the smaller were compared with spermatozoa and the larger with ova. Different stages of the development of the "ova" into young Miliolas were found. These became free when invested by a spherical shell. This phase of reproduction was observed in September and October.

After the winter Miliolas were again found giving rise to young, but now the process appeared to be asexual, none of the spermatozoa-like bodies being found.

A species of *Miliola* from Heligoland was kept in vessels of sea-water. After some weeks rounded heaps some 2 millims. in diameter were found at the bottom of the vessel. These were invested by a firm wall covered with sand, and contained several alveolar spaces. In some examples the spaces contained numbers of bodies resembling *Euglenæ* in their shape and movement, though no flagellum was observed. In other cases the alveoli contained undivided protoplasm, or they were empty, or they contained young shells, one to each alveolus, which presented some resemblance to young *Miliola* shells. The further development of these shells was, however, not observed. SCHNEIDER'S observations require confirmation before they can be accepted.

In 1879, LANKESTER (20) described a number of "egg-like bodies" in the protoplasm of *Haliphysema tumanowicsii*, BOWERBANK, having a diameter varying from $\frac{1}{500}$ to $\frac{1}{1500}$ inch ($51 - 17\mu$). The larger masses were nucleated, but the smaller were said to be devoid of a nucleus. It was conjectured that these bodies are in some way concerned with reproduction.

In the following year, 1880, MUNIER-CHALMAS (24) stated

as the result of the investigations of four fossil species of Nummulites and two of the allied genus *Assilina*, his conclusion that these species were dimorphic, and that probably the phenomenon of dimorphism was general. This conclusion was based on the fact that Nummulites occurring in the same strata, and having identical external characters, fall into two groups. These differ from one another, first, in the size of the whole disc; second in the size of the central chamber. On breaking them open it is found that the small ones have a large central chamber, and the large ones a small central chamber. Intermediate forms, it was stated, do not occur. Although the superficial markings are alike in the two forms, they had hitherto been reckoned as distinct species.

Relying on the fact that only large examples of the forms with small central chambers had been found, MUNIER-CHALMAS concluded that each species consisted of two sets of individuals; first, those with a large central chamber, which attained a small size, and whose development was arrested at this stage; second, those in which the size was increased by the addition of chambers at the end of the spiral, while the large central chamber was replaced by a prolongation of the spire of chambers to the centre of the shell.

D'ARCHIAC and HAIME (1) had described the two kinds of arrangement of the central chambers in this family, and pointed out the corresponding difference in the size of the whole shell. These characters are referred to (pp. 63, 64, and 77) as indicative of different species, though this view is not consistently followed throughout.

The view stated by MUNIER-CHALMAS, that the two types represent different forms of the same species, had been previously expressed, though less definitely, by PARKER and JONES (27 a). These authors, on commenting on D'ARCHIAC and HAIME's ' Monographie,' refuse to recognize the mode of arrangement of the central chambers as a character on which to separate natural groups, and state their opinion that the forms of small size, with a large central chamber are "free growing individuals soon arriving at their limit of growth."

The existence of the two closely associated forms had also been previously recognized by DE HANTKEN and DE LA HARPE. DE LA HARPE, in a letter to Professor RUPERT JONES, dated Oct. 1, 1879 (19 *a*, p. 91), states a "general law of the distribution of Nummulites, according to which the characteristic species of a bed are always two of the same zoologic group, of which the larger has no central chamber" (distinguishable by a lens) "and the smaller always has one." In illustration eight pairs of species thus associated are given.

In 1881, DE LA HARPE (15), expressing his own views and those of DE HANTKEN, commented on MUNIER-CHALMAS' paper.
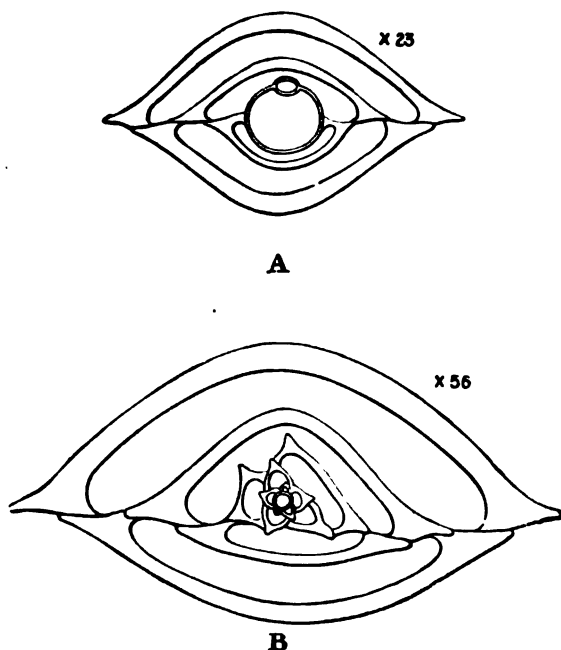
Biloculina depressa, D'ORB. Sections of the shell—

A. Of the megalospheric form. (Megalosphere 200–400 μ.)

B. Of the microspheric form. (Microsphere 20 μ.) The two terminal chambers are omitted in B.

(MUNIER-CHALMAS and SCHLUMBERGER, 25.)

While agreeing that the two forms constituting a "pair" resemble one another in the external sculpturing, he points out that examples intermediate in size between them do occur, and also small examples with a small central chamber. It is also shown that the two forms differ in the characters of the chambers which make up the inner whorls as well as in the size of the central chambers. While the view that one form results from the modification of the other is thus shown to be untenable, it is suggested that they might with more reason be regarded as representing two sexes of a species. The authors, however, do not definitely abandon the old idea of the specific distinctness of the two forms.

In 1883, MUNIER-CHALMAS and SCHLUMBERGER (25) communicated to the Académie des Sciences the fact that the phenomenon of dimorphism occurs also in several species of the Miliolidæ. Thus, in *Biloculina depressa*, D'ORB., there are two forms (see wood-cut, p. 114): A, with a large central chamber 200–400 μ in diameter, and with an outside diameter of the shell of 2·10 millim.; and B, with a small central chamber 20 μ in diameter, and an outside diameter varying from 1·5 millim. to 2·64 millim. The interesting fact was also brought forward, that in this group there is a very marked difference in the mode of growth of the two forms. While in the form A, the arrangement of the chambers following the central one is biloculine from the first, in the form B the chambers following the minute central chamber are arranged at first on the quinqueloculine plan, the biloculine arrangement not being attained, in *B. depressa*, until the eleventh chamber is formed.

A similar dimorphism is stated to exist in the genera *Dillina, Lacazina, Fabularia, Triloculina, Trillina, Quinqueloculina, Pentellina, Heterillina,* and *Alveolina* among the *Imperforata,* and among the *Perforata* in the genera *Nodosaria, Dentalina, Siphogenerina, Rotalina,* and *Amphistegina.*

In the same year SCHACKO (29) described a dry specimen of *Peneroplis proteus,* D'ORB., many of whose chambers contained numbers of young shells. These consisted of an oval central chamber measuring some 35 μ in long diameter, and a canal-

like second chamber. The central and second chambers of the parent shell are represented as exactly resembling in size and shape those of the young.

In 1884, BRADY'S magnificent monograph (1 a) on the Foraminifera appeared in the "Challenger" Reports. The work deals mainly with the classification and distribution of the Foraminifera, their life-history being little noticed. There are, however, two records in it which bear upon the matter.

A specimen of *Cristellaria crepidula* (FICHT. and MOLL. sp.) is described and figured (Plate 68, figs. 1 and 2), which contained young shells in three of the terminal chambers. The parent shell is megalospheric, the megalosphere being pear-shaped, and measuring $110 \times 84 \mu$. The young shells consist of a spherical or somewhat triangular chamber varying in size from 60 to 30 μ, to which in some cases a second smaller chamber is added.

In the description of *Cymbalopora (Tretomphalus) bulloides*, D'ORB., in which the shell of small chambers, arranged in an irregular spiral, is completed by an enormously inflated terminal chamber, it is stated, on the authority of Dr JOHN MURRAY (p. 639), that in every specimen from the surface which was examined, "the shell was filled with minute monadiform bodies."

In a paper (26) published in 1885, MUNIER-CHALMAS and SCHLUMBERGER introduced the terms *Mégasphère* and *Microsphère* for the central chambers of the two forms of a species.

In October, 1888, BRADY (2) described specimens of *Orbitolites complanata*, LAMK., var. *laciniata*, BRADY, collected in Fiji, whose large peripheral chambers were crowded with young megalospheric individuals. Such specimens had been previously recorded by W. K. PARKER.

In BRADY'S specimens the parent form was microspheric. Vertical and horizontal sections of the shell are figured, showing the small chambers continued to the centre. It is pointed out that these shells differ from those whose centre is occupied by a primitive disc (the megalospheric forms, *cf.* fig. 45), not only in the absence of the primitive disc, but in the

fact that the thickness of the shell at the centre is only one-third of that of the megalospheric form.   However, in alluding to the question of dimorphism, BRADY considered that the evidence of *Orbitolites* supported the view suggested by MUNIER-CHALMAS that the microspheric form was a modification of the megalospheric.

In 1890, SCHLUMBERGER (35) described *Adelosina polygonia,* a new species of the Miliolidæ.   From the figures it appears that the dimensions of the megalosphere and microsphere of this species are, in particular instances, 216 μ and 25 × 18 μ respectively.   The plans of growth of the two forms are different throughout, the megalospheric forms having the chambers arranged (in 99 cases out of 100) in a triangular, while the microspheric forms have them arranged in a quadrangular figure.

Among the specimens examined the frequency of occurrence of the megalospheric and microspheric forms was as 8 to 1.   In fully-formed shells the microspheric form is slightly smaller than the megalospheric (microspheric form 1·4 mm., megalospheric form 1·5 mm. in diameter).   Young specimens of the microspheric form occur.   It is pointed out that in this case the view suggested by MUNIER-CHALMAS, and adopted by the author, that the microspheric is a development of the megalospheric form, is clearly untenable.

In May, 1893, VAN DEN BROECK (5) published his "Étude sur le dimorphisme des Foraminifères," in which the relationship of the two forms is discussed.

In this work the author reviews the evidence on the subject of dimorphism, and the reasons for regarding the two forms as distinct from their origin are urged with much force.   It is shown that the difference in the size of the central chamber indicates a difference in the reproductive processes by which the two forms originate.

In speculating as to the nature of this difference VAN DEN BROECK puts forward the view, which, as is stated, had previously been suggested by DOLLFUS ('Annuaire Géologique,' 1890, p. 1099), that the megalospheric young are the result of

" endogenous gemmation," and the microspheric young of "ecto-genous fission." Both processes it is conceived might be going on simultaneously in one individual. The author has unfortunately revived, in support of his hypothesis, the old idea of the individual distinctness of the contents of the different chambers of the foraminiferan shell. Apart from this, however, the view as to the mode of origin of the two forms of young cannot be accepted as correct. For, as will be shown below, in the cases in which the origin of the megalospheric young has been traced (*Polystomella, Rotalia*), they have arisen by the multiple fission of the whole of the protoplasm of the parent. The exact origin of the microspheric form is still unknown, but the zoospores from which it is probably in some way derived, are also produced (in *Polystomella*) by the multiple fission of the parent protoplasm.

(b.) *The Relation of Orbulina and Globigerina.*

The features presented by *Orbulina* have been much discussed (*cf.* BÜTSCHLI (6), pp. 68–70), and as they have been supposed to exemplify the phenomenon of dimorphism, the subject claims our notice here.

POURTALES (28) first drew attention, in 1858, to the fact that a spirally arranged group of chambers, resembling the complete shell of a *Globigerina*, is often found within the spherical shell of *Orbulina* (*cf.* wood-cut, p. 119). This he considered to be the young of *Orbulina*, and he suggested that *Globigerina* and *Orbulina* might be alternate generations in the life-history of one species.

In 1868, Major OWEN (27) stated his opinion that the *Orbulina* shell "may be regarded as a wild-growing closing-in chamber " of the *Globigerina*.

In 1883, SCHACKO (29) described specimens of *Orbulina*, both recent and fossil. He showed that the *Orbulina* shell is sometimes double ; that the contained *Globigerina* shell is most fully developed when the *Orbulina* shell is small, and that in large (dry) specimens a heap of thin-walled fragments is often

all that remains of it.   He considers that the *Globigerina* shell
is gradually absorbed, and ultimately disappears.   With regard
to the contained *Globigerina* shell it was shown that, as in free
living *Globigerinæ*, its terminal chambers are frequently covered
with spines, and that these reach to the *Orbulina* shell and fuse
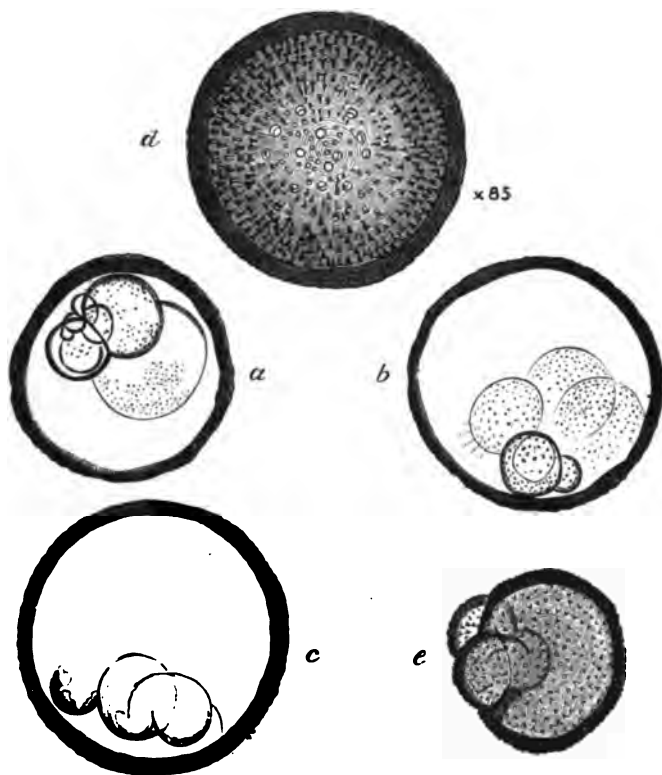
Orbulina universa, bottom specimens, Brady Collection, *Globigerina-Orbulina*
series.   × 170.

a–c. *Orbulinas* with contained *Globigerina* chambers (represented in optical
section). These are seen in different stages of absorption. The spines are
only seen in *b*.

d. An empty *Orbulina* shell.

e. A specimen in which the *Orbulina* shell does not completely enclose the
Globigerina chambers.   ·

with it; they are, however, exceedingly slender. The chambers composing it may be as many as thirteen. The diameter of the apical chamber varies from 16 to 23 μ.

SCHACKO found some small bodies "resembling in shape and size" the first two chambers of the *Globigerina*, especially abundant in the terminal chamber of the latter. These he regarded as young.

In April, 1884, SCHLUMBERGER (34) presented a note to the Académie des Sciences in which he urged the view that the empty *Orbulina* shell and that with *Globigerina*-like contents, were dimorphic forms of the same species, comparable with the forms which had been shown to exist in the species of Nummulites and Miliolids. After reviewing the evidence he proceeds as follows (p. 1004):—" La loge unique de *l'Orbulina* est l'homologue de la loge initiale des autres Foraminifères : lorsqu'elle reste vide, elle est de la forme A; avec la série de loges internes elle est de la forme B."

SCHLUMBERGER concludes with the remark that the case of *Orbulina* is in favour of the view that the forms A and B are distinct from their origin.

The ascertained facts appear to be as follows:—

In a sample of the shells of *Orbulina* many of the individuals are simple empty spheres varying in size, and the largest shells of the sample are of this character. In others, the interior of the sphere is more or less completely occupied by a spire of chambers closely resembling a free *Globigerina* shell. This is firmly attached to the wall of the investing spherical chamber. In rare instances (*e*, wood-cut) the *Orbulina* chamber does not completely enclose the *Globigerina* chambers, and in that case the outer spherical surface of the *Orbulina* is interrupted by the prominences formed by the terminal chambers of the *Globigerina*. Usually the *Globigerina* shell is remarkable for the extreme tenuity of its walls and spines, but when portions of it are not enclosed by the *Orbulina* shell, they are found, as SCHLUMBERGER points out, to be thick walled, while the enclosed portions are thin (*e*).

The *Globigerina* chambers are usually most perfect when

the investing chamber is small, the larger this chamber is the less perfect are the contained chambers. In dead specimens these are frequently represented by a mass of broken fragments. In the largest *Orbulinas* no trace of contained chambers is found.

A small chamber whose diameter varies, according to SCHACKO, from 16 to 23µ is frequently found at the apex of the spire of chambers.

While the *Globigerina* chambers are perforated by small apertures of uniform size, the pores of the *Orbulina* are of two sizes.

It not unfrequently occurs that the *Orbulina* shell is double or even treble, the spheres being contained one within the other, and unattached, as in a Chinese carving.

Before discussing the evidence, it will be well to recall the mode of life of *Orbulina*.

In common with the rest of the family *Globigerinidæ*, and species of the genus *Pulvinulina* among the *Rotalidæ*, *Orbulina* is frequently found leading a pelagic existence at or near the surface of the sea. When taken in the tow-net, it is often beset with long spines which may be more than three times the diameter of the shell in length. When the protoplasm is extended a thick vacuolated layer invests the shell and the bases of the spines.

The fact that all transitional stages are found between small *Orbulina* shells containing a perfect spire of chambers, and large ones which are empty, appears to point to the conclusion that the empty *Orbulina* shells when small contained such chambers.

What is the relation between the *Orbulina* shell and the contained chambers? The suggestion that these constitute a young individual about to be set free is incompatible with the facts (1) that they are attached to and sometimes involved in the *Orbulina* shell; (2) that they are often seen in stages of degeneration; and (3) that the largest *Orbulina* shells are empty and complete.

According to Major OWEN's view, the outer sphere may be

regarded as a "wild growing closing-in chamber," and it appears probable that this is the correct interpretation. The *Globigerina* chambers, with their radiating spines, are probably invested with vacuolated protoplasm before the *Orbulina* chamber is formed, as the *Orbulina* shell is afterwards. When the growth of the shell has reached a certain stage by the addition of chamber to chamber on a spiral plan, a spherical chamber is formed concentric with the surface of the investing protoplasm. This may completely enclose the chambers already formed, or parts of these may, in rare instances, project beyond it. At a later stage a second and a third shell may be added while the contained chambers are absorbed.

[Since this was written RHUMBLER has published a preliminary account (28 c) of his investigations of *Orbulina*, in which he arrives at the same conclusion with regard to the relation of the *Orbulina* shell to the contained chambers.]

The formation of such a large terminal chamber, as Major OWEN pointed out, is not peculiar to this form. As mentioned above, in specimens of *Cymbalopora* taken at the surface, the spire of small chambers is completed by a large inflated chamber far exceeding in volume the rest of the chambers taken together.

If this view of the relation of the *Orbulina* shell to the enclosed chambers is correct, it is clear that the idea that the empty *Orbulina* shell, and that enclosing the *Globigerina* chambers correspond respectively to the megalosphere and microsphere of other Foraminifera, is untenable. As M. SCHLUMBERGER has done so much to show, it is to the first formed chambers that we must look for the characters which distinguish the two forms, and the first formed chambers are surely those, as in all other cases, which occupy the apex of the spire. It follows that, unless it is shown that other characters distinguish the forms, only those specimens of *Orbulina* in which the contained chambers are complete can furnish evidence of dimorphism.

With regard to the relationship of the free *Globigerina* shell to *Orbulina*, I have very little evidence to offer. The first chamber of the free *Globigerina* is about the same size as that

of the *Globigerina* chambers included in *Orbulina*. In 63 surface specimens of *Globigerina* mounted in balsam, in the Brady Collection, the mean diameter of this chamber varies from 7 to 20 μ, the most frequent diameters being 14 and 17 μ. SCHACKO gives the diameter of the first chamber of the *Globigerina* enclosed in the *Orbulina* shell as 16 to 23 μ. So far as this rather scanty evidence goes, then, it appears that there is no evidence of dimorphism in the central chambers of these forms.

It will be shown below that in the species which I have examined the two forms are as sharply distinguished by the character of their nuclei as by the size of the central chambers. The only evidence on this head with which I am acquainted is that of one specimen of a free *Globigerina bulloides* with eight chambers, described by R. HERTWIG (17), in which a single large nucleus was present. From analogy it would appear that this specimen was megalospheric.

Further evidence on the nature of the nuclei of *Orbulina* and *Globigerina* would no doubt throw light on the question of their relationship.

(c.) *Nuclei.*

Our knowledge of the nuclei of Foraminifera is mainly derived from the descriptions of R. HERTWIG, F. E. SCHULZE, and O. BÜTSCHLI.

The evidence is for the most part of a fragmentary character, but it may be convenient to bring it together. The observations which I have met with are here arranged under the names of the families.

I. *Gromidæ.*—In *Gromia*, MAX SCHULTZE ((38), p. 22) found a single nucleus in young specimens, and from two to sixty in old ones.

II. *Miliolidæ.*—In *Quinqueloculina fusca*, F. E. SCHULZE ((41), p. 136) described an oval body which he took for the nucleus.

In a species resembling *Spiroloculina hyalina*, F. E. SCHULZE, R. HERTWIG ((16), p. 46) found a single nucleus in young specimens, and as many as seven in one with four chambers.

Among the *Peneroplinæ*, BÜTSCHLI ((7), p. 80) found a single nucleus in two specimens of *Peneroplis pertusus*, FORSK., but in a third specimen as many as four were present. The central chambers of the specimens (which appear to have had a mean diameter of 29 to 34 μ) are considerably larger than those which succeed them, and are of the same size as that of SCHACKO'S specimen described above (p. 115). It is probable therefore that they belonged to the megalospheric form.

In an example of the type of *Peneroplis planatus*, F. and M., whose central chamber measured about 27 μ in diameter, and hence would appear to have belonged to the same form, some eighteen or twenty nuclei were distributed through the protoplasm.

In *Orbitolites complanata*, LAMK., BÜTSCHLI ((7), pp. 80–82) described numbers of small round or oval or irregular nuclei in which a reticular structure could be detected. They were most numerous in the peripheral chambers, and might be absent from the central chambers. As will appear below, this description differs considerably from what I have found to be the usual condition either in the megalospheric or microspheric form of this species.

III. *Astrorhisidæ.*—In *Dendrophrya radiata*, WRIGHT, MÖBIUS ((23), p. 13) found a single large nucleus, 66 μ in diameter.

IV. *Lituolidæ.*—No record.

V. *Textularidæ.* BÜTSCHLI ((7), p. 83) described two specimens of this genus whose central chambers appear to have measured about 12 μ in diameter, and which, therefore, may have belonged to the microspheric form. In one, which was young (nine chambers are represented), a single nucleus was present; in the other, which had fourteen chambers, at least three were present.

R. HERTWIG ((16), p. 50) found a single nucleus situated in the first formed chamber in a specimen of this genus with five

chambers, and in another specimen, with thirteen chambers, one nucleus was also present.

VI. *Chilostomellidæ.*—No record.

VII. *Lagenidæ.*—A single round nucleus is described in species of the genus *Lagena*, by M. SCHULTZE ((38), p. 56), F. E. SCHULZE ((42), p. 14), GRUBER ((14), p. 501), and BÜTSCHLI ((7), p. 83). In BÜTSCHLI'S figure a coarse nuclear reticulum and rounded nucleoli are represented.

VIII. *Globigerinidæ.*—A single large nucleus containing granules, is described by R. HERTWIG ((17), p. 345) in a specimen of *Globigerina bulloides*, D'ORB.

IX. *Rotalidæ.*—In *Spirillina vivipara*, EHRB., BÜTSCHLI((7), p. 84) described numbers of minute stained bodies distributed through the protoplasm. Some of these he considered to be nuclei, while others were regarded as stained portions of food material.

In *Discorbina*, sp., numbers of bodies regarded by this author as probably nuclear in nature, were found in the protoplasm ((7), p. 86).

In a species belonging to the Rotalidæ, R. HERTWIG ((16), p. 49) found a single nucleus in individuals whose chambers numbered from 1 to 3. The central chambers in these specimens measured from 27 to 35 μ in diameter. In examples with four chambers, from one to four nuclei were present. The size of the central chamber is not stated in these cases, but from the figures it appears that its diameter was about the same as in the examples mentioned above.

F. E. SCHULZE mentions ((42), p. 20) the occurrence of a single nucleus quite similar to that of *Polystomella* (see below) in *Rotalina*, sp.

In *Calcarina Spengleri* (LINN.), BÜTSCHLI ((7), p. 85) described and figured a single large nucleus, with a clearly-marked reticulum. Nucleoli were present in the peripheral zone, in three cases out of four. In some the nucleoli are said to have a fine reticular structure.

X. *Nummulinidæ.*—In *Amphistegina Lessonii*, D'ORB., BÜTSCHLI ((7), p. 86) also found a single large nucleus in one of the inner chambers. Some small bodies in the later chambers

are also mentioned, which it is suggested may have been of the nature of nuclei.

Polystomella striatopunctata, F. and M. SCHULZE'S account ((42), p. 18) of the nucleus of this species is the most complete that has yet been given. It is described as a round body having, in some cases, a diameter of 56 μ, and surrounded by a conspicuous membrane of considerable thickness. Highly refracting nucleoli, lying in a clear and apparently fluid substance, occupy the interior. In quite young specimens only one nucleolus was found, but they may number as many as twenty or more in advanced specimens. The nucleus occupies a position in the middle third of the series of chambers, and often lies partly in one of the narrow canals connecting the chambers, being preserved in its progress from one chamber to another. SCHULZE points out that the position of the nucleus is thus dependent on the total number of chambers.

Sometimes two, and in one instance three, nuclei were present, and in this case they occupied adjoining, or at least neighbouring, chambers.

VERWORN ((46), p. 462) has made a very interesting observation on the nucleus of *Polystomella*. On breaking an individual into pieces, he finds that, while many of the larger pieces remain alive, as shown by their extended pseudopodia, only the fragment containing the nucleus possesses the power of secreting fresh material to repair the broken shell.

HOFER ((19), p. 149) objected to VERWORN'S experiment on the ground that, in the Polystomellas investigated by him, by far the greater number of specimens had many nuclei, so that when a shell is broken it would be improbable that any considerable fragment would be free from nuclei. I can only say that HOFER'S experience is very different from mine, as it will appear later.

At first sight much of the evidence here collected appears contradictory.

It will be shown below that in *Polystomella* the megalospheric form has a single nucleus during the greater part of its

existence, and the microspheric form numbers of comparatively small nuclei.

Some of the apparently contradictory statements may probably thus be reconciled. Thus, in *Textularia*, while MAX SCHULTZE and BÜTSCHLI find two, three, or more nuclei, R. HERTWIG finds a single one. From BÜTSCHLI's figures it appears that he was dealing with microspheric forms.

The frequent occurrence of a single nucleus in the genera which have been examined is in harmony with the fact that the megalospheric form usually far outnumbers the microspheric. It is probable, however, that the nuclear history differs to some extent in different groups of Foraminifera. It may also be observed that, as I shall show presently in the case of *Polystomella*, bodies which I believe to be formed in the elaboration of the food may possess staining properties and be thus readily mistaken for nuclei.

In *Rotalina* and *Globigerina*, HERTWIG describes the nuclei as consisting of two parts, of which one is granular and takes the stain, and the other is clear and homogeneous. SCHULZE however states that the nucleus of *Rotalina*, as seen by him, resembles that of *Polystomella*, and this is also true of *Rotalina Beccarii* (figs. 39 and 40). In *Polystomella*, an appearance somewhat resembling that which HERTWIG describes is sometimes presented when a vacuolar space, probably resulting from the action of the reagents, lies alongside the nucleus.

At the conclusion of his paper, HERTWIG says that the Foraminifera, with one or few nuclei, would doubtless at the time of reproduction become many-nucleated. Relying on the analogy of the Radiolaria, with whose life history he had recently dealt (18), HERTWIG concluded that it is improbable that the multiplication of the nuclei should take place by simple fission, and that a process similar to that which he had found in *Thalassicola*, in which the originally single nucleus becomes divided into minute particles, which are distributed through the protoplasm, was more to be expected.

How correct HERTWIG's surmise appears to have been will be seen in the sequel.

2.

(a.) *Polystomella crispa* (LINN.).   Figs. 1–3 and 5–32.

In the hope of throwing light upon the life-history of
Foraminifera, I have examined a large number of specimens of
Polystomella crispa (LINN.), a species of almost cosmopolitan
distribution in shallow water, and abundant in the pools of our
own shores.

Methods.—In collecting material I have used a large horse-
hair sieve with bolting cloth fastened beneath it.   The sieve is
set in a shallow pool, and handfuls of seaweed are torn from the
rocks and shaken in the water standing in the sieve.   The
small creatures which live amongst the weed, including the
Foraminifera, fall through the meshes of the sieve and are caught
by the bolting cloth.

I have tried several reagents for killing the specimens, and
have obtained fairly satisfactory results with warm saturated
solution of corrosive sublimate and glacial acetic acid, in pro-
portions about 4 to 1.   The advantage of this reagent is that
the walls of the chambers of the peripheral whorl are rapidly
dissolved by the acid, so that it is not long before the proto-
plasm is killed.

After thoroughly washing in water, the specimens were
stained for some hours in picro-carmine.   By this means the
nuclei are stained bright red, and the protoplasm pale yellow.

Many specimens have been examined by means of sections,
but the majority have been mounted whole.

As has been shown to be the case in so many other Forami-
nifera, this species is dimorphic.   Externally the two forms are,
so far as I am aware, undistinguishable; but, on examining
decalcified and stained specimens, they may be at once referred
either to the megalospheric or microspheric form.

These differ from one another in respect of the size and
shape of the central chambers, and in respect of their nuclei.

The megalospheric form (fig. 13) has a large central chamber,

a second chamber of a characteristic shape, and, during the greater part of its existence, a single large nucleus.

The microspheric form (figs. 6 *a* and *b*) has a small central chamber, and a number of small nuclei distributed through the protoplasm.

As in other species, the two forms differ greatly in the frequency of their occurrence. Out of 1812 specimens which I had examined up to January 12th, 1894, 52 were microspheric, giving a proportion of megalospheric to microspheric forms of about 34 to 1. The relative proportion of the two forms varies, however, at different seasons.

Among the microspheric forms I have met with several young ones, which are far inferior in size and the number of their chambers to the large megalospheric individuals. (*Cf.* Figs. 6 *a*, 7, and 13, which are all magnified 170 times.)

Before describing the characters of the two forms, certain features common to both may be mentioned.

The Structure of the Protoplasm in Preserved Specimens.— When a live specimen of *Polystomella* is crushed under a cover-slip, and examined under a high power, the protoplasm appears as a colourless mass, containing granules, but not vacuolated.

In sections of specimens killed with osmic vapour, or any of the other reagents usually employed, the protoplasm is found to present an appearance which resembles that of bread, the granular solid portions forming walls and strands between rounded vacuolar spaces, which communicate with one another to a greater or less extent. This structure, for want of a better name, may be referred to as a reticulum.

In examining decalcified and preserved specimens as a whole, it is often seen that the protoplasm of one chamber protrudes into the next through the canals which connect the chambers together. These protrusions are marked by the lines of the reticulum. In the parts of the chambers away from the connecting canals the reticular structure is obscurely seen, but in the regions where such protrusions have occurred the strands of the reticulum are seen to be drawn out parallel with one

another in the canal, and, in the chamber beyond, to be disposed
concentrically around the aperture by which the protoplasm
has entered (fig. 1). These protrusions are frequently repeated
through successive chambers.

The movement of the protoplasm to which this effect is due
occurred, no doubt, solely as the result of the action of the
reagent used in killing it.

In many cases the nucleus is involved in one of these
movements of the protoplasm, a portion of it being carried
through into the succeeding chamber, where it is seen drawn
out, and, like the protoplasm which surrounds it, disposed
concentrically to the aperture by which it entered. Portions
may thus be carried through as many as three chambers from
that in which the main body of the nucleus lies (fig. 1).

Bodies other than the Nuclei contained in the Protoplasm.—
In Polystomellas collected in summer there are present in
about one specimen in five or six of the megalospheric form,
and also in specimens of the microspheric form, small bodies
of a rounded shape, which take a red stain with picro-carmine
(fig. 2). They are most abundant in the terminal chambers,
becoming fewer and fewer as the series of chambers is fol-
lowed backwards. In some cases they also increase in size
towards the terminal chambers. The size may vary from $8\,\mu$
in diameter to $1\,\mu$ and under, and in any specimen, though
frequently uniform, they may present considerable variations in
size. Sometimes they are so abundant as to form a prominent
feature in a stained specimen (fig. 2); in other cases they are
sparsely scattered through the protoplasm, and, as stated above,
they are absent altogether in the majority of specimens. These
statements hold true of examples killed and stained in a batch,
so that the differences cannot be dependent on different modes
of treatment.

Though generally spherical, they sometimes present an
elongated shape, and they may be excavated by deep concave
indentations (fig. 3), which may be so extensive as to reduce
the body to a hollow shell of stained material.

While they are generally uniformly stained, in some cases

stained and unstained regions, variously distributed, may be detected. In sections of specimens stained with picro-carmine, and afterwards with methylene blue, they retain the red stain, while the surrounding protoplasm is stained blue.

They are at least as frequently met with, and in that case they are as abundant, in young individuals as in old ones.

In a batch of specimens of *Polystomella* collected in October, and kept in dishes of sea-water for some months, these bodies are found, after the usual preparation, to be almost entirely absent. The water in which the Polystomellas were kept contained numbers of Infusoria, and some small clumps of brown algæ, which may have served as food. Although the protoplasmic contents of the shell may have shrunk during the period that they were submitted to these conditions, and their nuclei, as will be shown later, underwent a very marked diminution in size, few or none of the specimens died. Out of 116 examples only four showed any indication of the bodies under consideration. Some of the specimens were killed in January (after three months' captivity), and the remainder in March (after five months); and, with the second set, examples freshly collected from the sea were killed and stained, using the same solutions for all. In those fresh from the sea the stained spheres were more abundant, though fewer than in specimens collected in summer.

How are these bodies to be regarded ?

It appears probable that they are either of nuclear nature, or that they are food material in some stage of metabolism.

In favour of their nuclear nature is the fact that with the reagents which I have used they have the same staining reactions as the nuclear elements.

On the other hand against their nuclear nature many considerations may be urged.

They are generally (at least in four cases out of five) absent altogether from specimens in which the large nuclear elements are well stained, and their presence or absence appears to be entirely independent of any change which may be seen in these nuclei. They may occur in both microspheric and megalo-

spheric forms, whose large nuclear elements are so strongly contrasted, and in both young and old specimens.

In favour of the view that they are food stuff are the facts that they are always most abundant in the terminal chambers, through which the greater part of the food taken in must pass before it is elaborated into protoplasm, and that, as above stated, they are to a large extent absent from specimens kept under conditions unfavourable to nutrition.

In the Infusorian *Balantidium entozoon* (EHR.), which inhabits the rectum of the frog, bodies which appear to be of a similar nature are often present (fig. 4, *a* and *b*). In preparations (made in March) killed with osmic vapour, and stained with picro-carmine, the macro-nucleus is deeply stained, and what appears to be the micro-nucleus may generally be detected lying in a depression in it. In some specimens no other stained bodies are present, but in most cases numbers of round bodies with a deep red stain are thickly scattered through the protoplasm. They vary in size from 1 to 5 μ or more in diameter, and while many are uniformly stained, in others darkly stained bodies are seen to lie in a clear or granular matrix (fig. 4 *b*).

Considering the quiescent condition of the macro-nucleus and the micro-nucleus in these specimens, the inconstant occurrence of the bodies, and the variety in size and constitution which they present, it appears impossible to entertain the view that they are nuclear, while the hypothesis that they are formed in the elaboration of the food material presents no difficulty, and is in accordance with other observations.

Miss GREENWOOD (13) has described in the endoderm cells of *Hydra* certain "nutritive spheres," which take a pink stain with picro-carmine, and which, as the name given to them implies, there is good reason to believe are formed in the metabolism of the food materials.

On these grounds I regard the stained bodies in question met with in *Polystomella* as nutritive in nature, formed, that is to say, in the elaboration of the food.

It must, however, be stated, that I am unable by the methods which I have hitherto employed to distinguish them from the

small nuclei which are found in the protoplasm in the later stages of the megalospheric form.

Besides these bodies which are stained by picro-carmine, several others are commonly present in the protoplasm. Among these may be mentioned :—

(1) Clear transparent globules which swell in water, and give the appearance of concentric light and dark bands with transmitted light; they are 3 to 4 μ in diameter, and do not stain violet with iodine.

(2) Dark yellowish-brown globules, having a diameter of 4 μ and under. They are sometimes present in large numbers (fig. 5).

(3) Pale yellow bodies of the same diameter, but less highly refracting than the last.

Radial arrangement of the Reticulum about the Nuclei.—In many cases, both in the megalospheric and microspheric forms the strands of the protoplasm are set in radiating lines about the nuclei (figs. 10 and 23). On examining whole specimens of the megalospheric form after decalcification, it is often seen that the outline of a chamber is indented opposite the nucleus. This effect must be due to the shrinkage of the nucleus after the wall of the shell is dissolved, the shrinkage of the nucleus having been greater than that of the protoplasm as a whole. The effect of this shrinking must be to produce a radial arrangement of the strand of the reticulum about the nucleus. It appears impossible in preserved specimens to distinguish such an artificially produced arrangement from any slightly-marked radiating disposition of the protoplasm which may exist naturally.

THE MICROSPHERIC FORM (figs. 6–12). The *Microsphere* is a nearly spherical chamber, whose diameter varies in different specimens from 6·5 to 13 μ. The average of the mean diameters in twenty-seven cases is 9·6 μ.

The second chamber is of the shape of a somewhat curved cone, and is applied to the microsphere by its concave side, communicating with it by a short canal at or near its apex. In

some cases there is an indication of a globular swelling near the apex of the cone, and this might be considered to be the second chamber, the remainder of the cone being the third. The succeeding chambers gradually increase in size, but the cog-like "retral processes" (see fig. 13) characteristic of the genus do not appear for some distance along the series of chambers.

The spire in which the first few chambers are disposed is often not flat, as in the succeeding chambers, but helicoid. When this is the case, the direction of the spire is sometimes dextrotropic and sometimes leiotropic.

Though the size attained is not larger than that of the megalospheric form, the number of chambers in specimens of the two forms of equal size is greater in the microspheric. This is owing to the fact that in this form the central region is occupied by small chambers which gradually diminish in size to the microsphere, while in the megalospheric form, a single large chamber, the megalosphere, occupies the centre.

The smallest specimen I have seen (fig. 7) has twenty chambers, and measures 220 μ across the short diameter of the spire of chambers; one of the largest has forty-seven chambers, and measures 800 μ.

Nuclei.—Microspheric individuals have many nuclei. They are distributed through many chambers, beginning at one of the internal chambers, and extending some distance beyond the middle of the series, counting from the microsphere to the terminal chamber. Thus, in a specimen with twenty-nine chambers there are twenty-eight nuclei extending from the fourth to the twenty-third. In one with forty-two chambers, there are forty-four nuclei extending from the thirteenth to the thirty-first.

There may be one, two, or as many as six nuclei present in one chamber, and on the other hand a chamber may be free from nuclei while the adjoining chambers contain them. I have never seen the nuclei extending into the terminal chambers.

The nuclei are generally of a round or oval shape. In nearly every case they are small in the inner chambers, and

gradually increase in size as they are situated further along the series. Thus, in one specimen, the innermost nucleus measures $30 \times 20 \, \mu$, and the outermost $48 \times 38 \, \mu$.

Structure of the Nuclei.—In sections the nuclei appear to consist of a homogeneous substance which stains moderately deeply with picro-carmine, with deeply stained nucleoli, round or oval, embedded in it. The nucleoli vary much in size and number, and when large may contain round vacuolar spaces with clear unstained contents (figs. 8 and 9). The large nuclei contain larger nucleoli than the small ones. Externally the homogeneous inter-nucleolar substance does not appear to be limited by a membrane or wall of any kind, but terminates sharply against the coarse reticulum of the surrounding protoplasm.

Division of the Nuclei.—Very often the nuclei are disposed in pairs in the protoplasm, and in some cases the opposed surfaces are flat and corresponding, as though marking a plane of division (figs. 9 and 10).

In a specimen of one of the microspheric individuals which was cut into sections, a nucleus in process of division is seen (fig. 11, a–c) in three consecutive sections. It so happens that the plane of the sections passes nearly at right angles to the plane of division of the nucleus. In the first section both divisions of the nucleus (which I will distinguish as right and left) are seen united by a constricted portion, and the right division appears larger than the left. In the next section a similar appearance is presented, but now the left is larger than the right. In the third section the left half alone appears. The nucleoli and the inter-nucleolar substance present exactly the same appearance as in nuclei which are not undergoing division.

It may, I think, be taken as a fact that the nuclei of the microspheric form increase in number during the earlier stages of growth by simple division.

Dispersal of Nuclear Substance.—Besides the round or oval nuclei, there are very generally present in the protoplasm irregular strands of red-stained substance. These may be small

and few in number, or they may be so large and abundant that the chambers containing them appear under a low power red with the irregular deeply stained masses. In sections these strands are frequently seen to be continuous with the nuclei (fig. 12).

In some specimens (fig. 6, *a* and *b*) the nuclei furthest removed from the centre present the rounded shape above described, several of them being disposed in pairs as though recently divided, but as the series of chambers is followed toward the centre the nuclei assume an irregular shape, and the red-stained strands appear in the protoplasm about them ; gradually the nuclei become more and more irregular, until in the innermost chambers no nucleus of the rounded form is seen, but in their stead there are the irregular deeply stained strands. In one large specimen, with forty-seven chambers, no rounded nuclei are visible, and the whole of the stained matter appears to consist of the irregular strands.

It has been stated that the rounded nuclei have not been observed in the terminal chambers, but this is not the case with the strands. Though in the majority of cases these are most abundant in the chambers in which the rounded nuclei lie, in others they are found in the terminal chambers, and in one specimen they are seen to be closely massed in the terminal chamber.

To repeat, the facts which the preparations show are these :—

1. The irregular strands may be seen continuous with the rounded nuclei.

2. In a single specimen all transitions are found between the rounded nuclei and the irregular strands.

3. While in some specimens, and especially young ones, only rounded nuclei are present and no strands, in others the reverse is the case, only strands being present and no nuclei.

It appears probable that while in young specimens the nuclear material is in the form of rounded bodies multiplying by simple division, it is gradually dispersed through the protoplasm in the form of these irregular strands.

[Since this was written I have examined specimens of the

microspheric form in the reproductive stage which is briefly described in Postscript 2, at the end of this Paper.

At the beginning of the process there described, before the protoplasm has emerged from the shell, numbers of nuclei as well as stained strands are present. The nuclei resemble in size and distribution those of a rounded form found in the vegetative phase, but they appear homogeneous, the nucleoli being very indistinct, or altogether absent. In view of the presence of these nuclei in the early reproductive phase, it appears doubtful whether, as above implied, and as stated in the preliminary Paper published in the 'Proc. Roy. Soc.,' vol. 56, p. 156, the whole of the nuclear material becomes distributed through the protoplasm in the previous stage.

I have no evidence as to the nature of the stained strands, and the part they play in the economy of the organism. I have simply attempted to describe the very remarkable condition which these microspheric forms present.]

THE MEGALOSPHERIC FORM (figs. 13–32).—The *Megalosphere*, which occupies the centre of individuals of this form, is a globular chamber varying considerably in size. Among eighty-nine examples, taken consecutively as they were collected, the diameter of the megalosphere lay between 60 μ and 100 μ in seventy cases. The greatest diameter among the eighty-nine cases was 165 μ, and the smallest 35 μ, and this is the smallest megalosphere that I have seen in any example of this species which I have examined.

The relations of the second and succeeding chambers to the megalosphere are shown in fig. 13. The second chamber is applied to the megalosphere for its whole length; at one end it is pointed, and at the other it abuts against the third chamber. The short canal by which it communicates with the megalosphere is usually situated near the middle of the concave side.

Nucleus.—A single large nucleus is present in the great majority of cases in the megalospheric form. When the nucleus lies completely in one chamber it is usually round or oval. In many cases, however, it is found to send one or more diverticula

into the succeeding chamber, as though fixed in the act of pass-
ing from one chamber to another (figs. 13, 15, and 23).

Position of the Nucleus.—As SCHULZE has shown (42), the
nucleus usually lies in or somewhere near the chamber which is
numerically in the middle of the series from the megalosphere
to the terminal chamber. There is some evidence to show that
its position depends, in part at least, on the disposition of the
bulk of the protoplasm. This is most clearly seen in young
specimens. It has been pointed out above that the megalo-
sphere varies considerably in size in different specimens. Now
in specimens with few chambers the megalosphere, being con-
siderably larger than the chambers which immediately succeed
it, contains a considerable quantity of the whole bulk of the
protoplasm. If in a young specimen the megalosphere is large,
the nucleus is found to be less advanced along the series of
chambers than in those in which the megalosphere is small. In
such specimens it appears that the nucleus tends to lie near the
centre of the protoplasm.

In specimens with twenty to thirty chambers, however, the
nucleus is generally found, as above stated, near the middle of
the series, and as the chambers which follow the megalosphere
successively increase in size, it is clear that its position is some
distance behind the centre of the whole of the protoplasm.

As will appear below, in dealing with other species whose
growth is spiral (*Rotalia, Calcarina, Truncatulina*) the nucleus
in like manner moves on from chamber to chamber as the
number of chambers increases. In *Orbitolites* and *Cycloclypeus*,
on the other hand, whose growth is cyclical, the nucleus in the
megalospheric form remains in or close to the first formed
chamber, which, owing to the mode of growth, is at the centre
of the protoplasm.

The Size of the Nucleus.—The nucleus increases in size as the
protoplasm grows. The truth of this statement may be realised
by inspecting the accompanying diagram (p. 140), in which the
results of the measurement of a number of examples are given.
The abscissæ indicate the diameter of the nucleus in μ's, and

the ordinates give the number of chambers (containing proto-
plasm) of the different examples whose nuclei were measured.

It must be observed, however, that these measures only
roughly indicate either the size of the nucleus or the bulk of
the protoplasm.   The nucleus is generally an oval body, and
the "diameter" here given is the mean between the long and
short diameters as it presented itself in the specimen.   In many
cases the nucleus would be seen endwise, hence the measure
of size here given is in many cases too small.   Again, the
number of chambers is only a rough indication of the bulk of
the protoplasm, for it takes no account of the size of the vary-
ing megalosphere, or of the fact that in many specimens the
terminal chambers are empty, a condition due either to their
contents having been extended in the form of pseudopodia, and
hence torn off when the specimen was collected, or to other
causes.

In the diagram two curves are given.   The upper one embodies
the results obtained with 118 specimens preserved fresh from
the sea in the months of May and June.   The lower gives the
results obtained from specimens kept in dishes in the laboratory
for three months, October to January.   The dots indicate the
average size of the nuclei of the individuals having the same
number of chambers, the number placed by each indicating the
number of individuals from which the average is taken.   It
will be seen that on the whole the direction of the curves is
upwards and to the right.   In other words, as the protoplasm
increases in bulk the nucleus undergoes a corresponding in-
crease.

In the specimens which had been kept alive in dishes the
nuclei are much smaller than in those killed fresh from the sea.
In these specimens so many of the terminal chambers were
empty that it appears probable that the protoplasm had shrunk
considerably as the result of the scanty food supply.   As I had
no means of measuring the extent of the shrinkage, the in-
dividuals are tabulated according to the actual number of
chambers which contained protoplasm when they were mounted.
The case is therefore rather understated, but the distance between
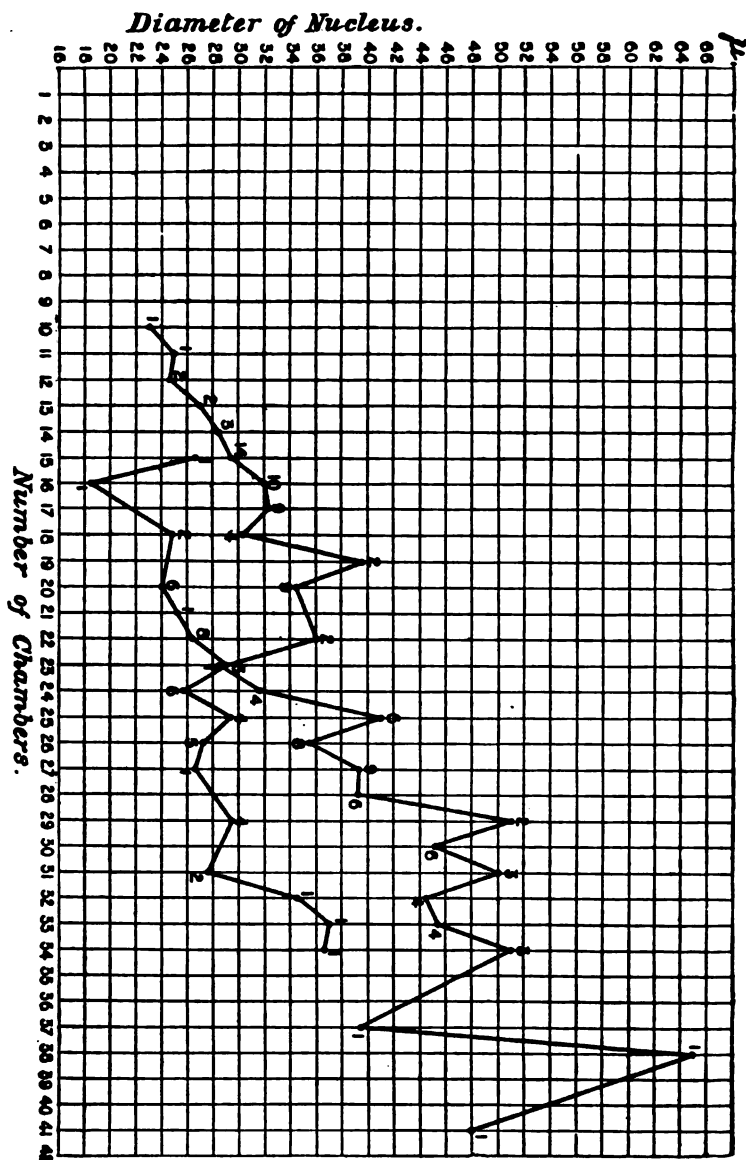
Table showing the increase in size of the nucleus accompanying the growth of the organism.

The abscissæ indicate the diameter of the nucleus, and the ordinates the

number of chambers containing protoplasm of the specimens whose nuclei are measured.

The figure placed by each dot shows the number of specimens having a given number of chambers, the average diameter of whose nuclei is here given.

The upper curve refers to specimens preserved fresh from the sea, the lower to specimens kept for three months with scanty food supply.

The curves overlap at one point, but do not cross.

the curves is sufficient to show the marked diminution in the size of the nucleus under the conditions in which the animals were kept.

Structure of the Nucleus.—In a section through the nucleus, which has been stained in picro-carmine, and in hæmatoxylin (fig. 14) or methylene blue, so as to give a contrast in colour between the nucleus and the surrounding protoplasm, the outline of the nucleus is generally sharp for the greater part of the periphery. It is not unfrequently the case, however, that there are regions where the sharpness of the separation is lost. This appearance I believe to be due to the fact that the plane of the section here cuts the nucleus obliquely.

Although, as F. E. SCHULZE states, the nucleus often appears to be surrounded by a definite membrane when seen in the whole specimen, and in sections has a well-marked limit (figs. 14 and 16), I have failed, in examining sections, to see a clear indication of a nuclear wall which is distinct from the protoplasm on the one hand, and the contents of the nucleus on the other.

Three elements are to be distinguished in the nucleus: the nucleoli, the reticulum, and the intermediate substance.

. The nucleoli appear to be invested by the substance which forms the reticulum, and the strands of the latter spring from this investment (figs. 14 and 16). They are round or oval bodies, staining readily with picro-carmine. They present great differences in different individuals. Their size in a given nucleus may be nearly uniform, or it may vary widely. If large, they generally contain one or more cavities (figs. 14, 18, &c.). Sometimes the nucleoli are compound *morula* like masses, whose appearance suggests that a large nucleolus is breaking up into a number of small ones (figs. 17 to 19), and frequently their dis-

position suggests that they have recently been set free by the breaking up of such a compound nucleolus (fig. 21). Young specimens always have large nucleoli, and it appears probable that the nucleoli become smaller as development advances.

The reticulum varies much in the closeness of its meshes. In some cases (fig. 16) it forms an open network, while in others its communications are so intricate and minute as to give the appearance of an almost homogeneous substance. This is especially the case in the shrunken nuclei of the specimens kept for some months in dishes.

Separation of portions of the Nucleus.—Very commonly in the chambers which lie towards the centre of the shell from that which the nucleus occupies—in the chambers, that is to say, through which the nucleus has passed as it has moved on with the growth of the individual—there are present fragments which take a pale reddish stain with picro-carmine, and hence are readily seen as they lie in the yellow stained protoplasm (fig. 24). The contour of these fragments is. generally indistinct, and in sections it is seen that they are more or less homogeneous granular bodies, while at their periphery they gradually acquire the reticular structure of the surrounding protoplasm. In some cases sections of the fragments show them to contain globular bodies, staining bright red with picro-carmine, which appear to be precisely similar to the nucleoli of the nucleus (fig. 25). In most cases, however, no such bodies are to be seen. These fragments lie as has been said in the track of the nucleus, and never extend far beyond it. In a few cases a prominence is seen in the profile of the nucleus as though a portion were being separated off (fig. 24).

From the appearance of these bodies, their position in the track of the nucleus, and from the fact that they may contain bodies like nucleoli, it seems probable that they are indeed fragments of the nucleus which have been given off into the protoplasm as it has moved on from chamber to chamber. It is to be observed that though these fragments sometimes contain nucleoli, the reticular structure is not seen in them.

Not unfrequently after treatment with picro-carmine, certain

portions of the protoplasm present a generally diffused flush. In many cases this flush cannot be seen, either by examination of the whole specimen or of sections, to depend on the presence of stained particles, though these may exist and be so small as to escape detection; the appearance is that the protoplasm in these regions has a general stain. Frequently the flushed region either extends from the central chamber to a little beyond the nucleus, or is limited to the chambers in the immediate neighbourhood of the nucleus. In the specimen from which fig. 23 is drawn the flush is present only in part of the chamber in which the nucleus lies, and here minute stained particles can be detected in the flushed region. Such an appearance suggests that minute portions of nuclear substance are being given off into the protoplasm.

Apparent Degeneration of the Nucleus.—In some cases the nucleus presents a different appearance from what has been described. Instead of possessing a rounded shape it may have the appearance of being partially collapsed, or it may be quite irregular, extending through several chambers, and sending rounded offsets into the protoplasm (fig. 26). This appearance is quite distinct from that produced by the change in shape which the nucleus undergoes when it is involved in a protrusion of the protoplasm, such as has been described above (*cf.* fig. 1).

Associated with this loss of its rounded shape is the absence or scarcity of nucleoli, and a general paleness, so that the characteristic red colour is only faintly indicated at the profile of the nucleus, the peripheral parts alone retaining their staining power, and this in a diminished degree. Such nuclei appear to be undergoing degeneration, having lost their shape, and, to a large extent, their nucleoli and their staining power.

Multiple Nuclei.—I have met with twenty-one cases in which more than one large nucleus is present in a megalospheric form. Sometimes this condition is associated with irregular growth; thus, in one example, where the inner chambers are very irregular in size and shape, there are seven nuclei. Three are present in another irregularly-grown specimen. In a case where there are two nuclei, the shape of the megalosphere

suggests that it was formed of two equal and incompletely fused or possibly incompletely separated spheres, to which apparently the nuclei correspond. In one specimen with seventeen chambers the nucleus is represented by seven pieces, distributed through the first seven chambers; in this case the megalosphere is very large (160 × 134 μ). There is no irregularity or peculiarity of growth in the remaining seventeen specimens. In two of them three nuclei are present, and two in the remainder.

The nuclei, when more than one are present, are generally about equal in size, and usually, though not always, situated in the same or adjoining chambers. The size of their nucleoli may be about the same, or the nuclei may present a marked difference in this respect. Thus, in one case in which two nuclei are present in one chamber, one contains vacuolated nucleoli, of 3 μ diameter, the other is crowded with minute nucleoli of a diameter of 1 μ. Two other cases presented a similar contrast.

The significance of the presence of more than one large nucleus in a megalospheric form will be discussed below.

Reproductive Phase. Formation of Zoospores.—Among Polystomellas collected between the end of March and the end of May, 1893, specimens are not uncommon in which the large nucleus is absent altogether. As an indication of the frequency with which these specimens occur, I may mention that among thirty-eight examples of megalospheric forms, collected on April 30, and stained and mounted without any selection, eight have no large nucleus.

These specimens generally present another conspicuous feature, namely, that the megalosphere in many cases communicates by broad channels with the adjacent chambers of the inner whorl, in addition to the usual communication between successive chambers. In the same way communications are found between the peripheral parts of the chambers of the inner whorl and those of the outer (fig. 32, *a*).

When treated with picro-carmine such specimens frequently stain a more or less deep pink colour throughout, though in some cases they remain pale.

Sections of these specimens generally show minute nuclei

scattered through the protoplasm of the terminal chambers. These are sometimes uniformly distributed, sometimes disposed in groups (fig. 30). In some cases these nuclei appear as compact, nearly uniformly stained bodies, in others they contain many round vacuoles (fig. 31). It may be observed that all the nuclei in such a specimen appear to be vacuolated to the same degree, whether it be much or little.

Two examples of the megalospheric form in which the large nucleus has disappeared (collected on May 31) present different conditions.

In one of these (fig. 27), which is composed of eighteen chambers, the whole protoplasm except that of the last two chambers is broken up into small spherical masses, 3 to 4 μ in diameter, the centre of each of which is occupied by a nucleus. The nuclei are in the phase of karyokinetic division (fig. 28), in which the chromatin elements have separated from one another, and present the appearance of two distinct parallel bands, 1·5 μ in length, separated by achromatic substance. From what is seen in the specimen next described it appears that the spherical masses are about to divide to form spores. In the two terminal chambers numbers of nuclei are present, but they are not in process of division, and the protoplasm though much vacuolated is not broken up into spheres. I am not able to account for this condition of the terminal chambers.

In the second specimen (fig. 32, a), which is composed of seventeen chambers, the whole of the protoplasm is divided up into spherical masses 3 to 3·5 μ in diameter. Each contains a nucleus, and a trabecular structure of the protoplasm can be seen in the interior. Between adjacent spheres a delicate network is seen, and in the terminal chambers a curved strand of this reticulum may here and there be detected, having the appearance of a flagellum (fig. 32, b).

Four days after this specimen was collected (June 4), I happened to be examining a partially empty shell under the microscope, and saw at one point through a transparent region of the wall of one of the chambers, an active movement in the interior. I crushed the specimen under a coverslip, and

numbers of actively moving spherical spores were set free in the water, while numbers of bodies, similar in all respects except their activity, remained among the broken fragments of the shell. On staining these with acid gentian violet indications of two flagella were made out, but the spores were too darkly stained for the nuclei to be detected. The spores were approximately of uniform size (4 to 6 μ in diameter), and, except for certain dark yellow masses, and some brown granules, constituted the whole of the contents of the shell.

It appears most probable that these actively moving spores are identical with the spherical masses seen in the preserved specimen last described. The difference in size may be accounted for by the difference in the modes of preparation.

. It will be noticed that while the masses in which the dividing nuclei lie have a diameter of 3 to 4 μ, the spores, which it appears are produced by the division of these masses, have an almost equal diameter (3 to 3·5 μ). It is probable that the spores owe their large diameter to the more vacuolated condition of their protoplasm.

On another occasion, the bodies which are represented in Fig. 33 *a* and *b* emerged from a specimen of *Polystomella*. At first I regarded these as *anisospores* produced by *Polystomella*, but I am now inclined to the view that they were produced by some other organism which had entered the shell.

The evidence afforded by the investigation of *Polystomella* may now be reviewed.

The *Microspheric form* occurs in various phases of development, both young and old specimens having been found (figs. 6 and 7). Numbers of small nuclei are present, scattered through the protoplasm, but not extending into the terminal chambers. Those in the inner chambers are smaller than those situated further on. The nuclei contain nucleoli of different sizes lying in an apparently homogeneous inter-nucleolar substance. The nuclei increase in number by simple division, and it appears

probable that they are so derived from a single nucleus. After maintaining their rounded form for a certain time, the nuclei give off portions of their substance, which become dispersed in the surrounding protoplasm.

Of the further history of the microspheric form of this species my preparations yield no evidence*.

The *Megalospheric form*, during the greater part—the vegetative period,—of its life, has a single large nucleus, which grows in size with the growth of the protoplasm, and passes on from chamber to chamber; moving towards the centre of the bulk of the protoplasm, though lagging some distance short of it. It contains a nuclear reticulum, nucleoli, which occupy the nodes of the reticulum, and a substance occupying the meshes. The nucleoli appear to increase in number and diminish in size with the advance of the organism. There is reason to believe that, as the nucleus moves on through the chambers, portions of its substance are given off into the protoplasm. It appears that this may occur either by the separation of considerable portions (figs. 24 and 25), sometimes containing several nucleoli, which lie strewn along the track it has followed, or by the dispersal of minute fragments into the surrounding protoplasm, causing a flush in the neighbourhood of the nucleus in the stained specimens (fig. 23).

What is the fate of the large nucleus? It might be supposed that it divides up by binary fission, and so gives rise to the small nuclei which are found later. As stated above, I have met with twenty-one cases in which more than one large nucleus is present, and in two there are as many as seven nuclei. Do these represent stages at the beginning of the process?

If there are twenty-one cases in which binary fission has begun and the segments into which the nucleus has divided are still large and few in number, the cases in which, by this process, many nuclei of smaller size have been produced, ought to be abundant. The fact is, that amongst the 1760 examples of the megalospheric form which have been examined (up to

* The mode of reproduction of the microspheric form is briefly described in Postscript 2.

January 12, 1894), including a large number in some stage of the reproductive phase, not one has presented itself which showed an intermediate condition between that with seven comparatively large nuclei and those with multitudes of minute nuclei of minimal size.

Although the conclusion is founded on negative evidence, it seems clear that the view that the small nuclei of the later stage are derived from the large nucleus by binary fission is untenable.

It seems not impossible that the presence of more than one large nucleus in the megalospheric form may be due to an accidental division having occurred in the process of passing from one chamber to another. The nucleus, which is a very plastic body, is often found with two or more processes extending into the chamber adjoining that in which the body of it lies, through the connecting canals. In the ordinary course, the nucleus must eventually take to one canal, any processes which may have extended into other canals being withdrawn, but it might occur if the forces propelling it onward were evenly balanced that a separation into two halves should take place. However this may be, I am inclined to think that the condition with multiple nuclei is not a necessary stage in the life-history, and may therefore to that extent be regarded as abnormal.

It appears probable that an indication of the fate of the large nucleus as an entity is given by those cases in which the nucleoli have decreased in number, its shape has become irregular, and its staining properties diminished (fig. 26). In such cases a large part of the substance of the nucleus appears to have passed into the protoplasm, while the remainder is in process of dissolution.

In what manner the nuclear material dispersed in the protoplasm becomes fashioned into the small nuclei of the later stage I have no evidence to show.

[RHUMBLER has recently published an account (28, *b*) of his investigation of *Saccammina sphœrica* (M. SARS), in which he has obtained a much more complete history of some of the nuclear changes than I have succeeded in doing.

RHUMBLER shows that the large solitary nucleus of this species is gradually altered during its growth. The *Binnen-körper*, the nucleoli of other authors, which in young specimens are few, large and frequently compound, after increasing in numbers at first, become in the later stages fewer or disappear altogether. Meanwhile chromatin granules appear in the nucleus, and increase in numbers, becoming embedded in *linin* fibres. In the course of development, the substance between the *Binnenkörper*, which is at first homogeneous, becomes vacuolated and then formed into a well-marked reticulum (*Wabenwerk*) which appears first at the centre, and gradually extends to the periphery of the nucleus. Finally, the nuclear wall, which has been very distinct in previous stages, disappears, and the linin fibres with the chromatin grains are dispersed in the protoplasm.

It is suggested that the last stage of this process is preparatory to reproduction.

There are clearly several points of resemblance between the nuclear changes of *Saccammina* and those of the megalospheric form of *Polystomella*. I find, on referring to my specimens, that minute granules are frequently present in the reticulum, which may very possibly be grains of chromatin, though they are not seen so distinctly as in the very large nuclei described by RHUMBLER. On the other hand, the nucleoli of *Polystomella* stain more readily with picro-carmine, and appear to retain their large size for a longer period than those of *Saccammina*.

Saccammina belongs to the family *Astrorhizidæ*, and builds a test which is generally single chambered, and is composed of foreign particles cemented together. This, as RHUMBLER clearly shows, is expanded to accommodate the growth of the contained protoplasm. Hence, the evidence of dimorphism, which is afforded by the first formed chambers of the shell in many multiloculate Foraminifera, cannot be present here. But it does not appear that there is evidence of dimorphism to be derived from the nuclei, whose condition in *Polystomella* and in the species described below, is so different in the two forms. Out of the 286 specimens examined by RHUMBLER, a single

nucleus was present in all but one (which had two nuclei, and was regarded as pathological), and the phases presented by the nuclei fall into a continuous series.

It is, of course, possible, though not probable, that RHUM-BLER did not happen to meet with the microspheric form, which is always the rarer, or that this form is in *Saccammina* so different from the megalospheric, that the two forms are not regarded as belonging to the same species. As the evidence stands however, it appears that we have in *Saccammina* a genus in which the differentiation into microspheric and megalospheric forms has not occurred. Its nucleus would not, therefore, be strictly comparable with the nucleus of the megalospheric form of a dimorphic species, such as *Polystomella crispa* (LINN.).]

In the second, or reproductive phase, minute nuclei (1 to 2 μ) are at first found scattered irregularly through the protoplasm in varying numbers (fig. 30), and broad channels of communication become opened up between the inner and outer chambers. The little nuclei are sometimes found as compact bodies, sometimes excavated by vacuoles, and the changes of which these conditions are the expression appear to be simultaneous throughout the animal.

It appears that, while the nuclei are sometimes readily stained by picro-carmine, they may pass through a phase in which they do not react to this stain, for specimens are not unfrequently met with in which the large nucleus has disappeared, and the direct communications between the chambers have become established, and which, therefore, appear to be in the reproductive phase, but in which no stained bodies of any kind are recognisable.

Ultimately the nuclei become evenly dispersed throughout the chambers and divide by karyokinesis, the protoplasm becoming aggregated about them in spherical masses (3·5 μ in diameter), each of which contains a dividing nucleus (figs. 27 and 28). At a later stage each nucleus, presumably the daughter nucleus of this division, becomes the centre of a flagellated zoospore (fig. 32, *a* and *b*). These are of approxi-

mately equal size.   Their diameter in specimens killed in cor-
rosive sublimate and acetic acid is 4 μ.

A simultaneous division of nuclei by karyokinesis imme-
diately before the formation of the reproductive elements, such
as occurs in the megalospheric form of *Polystomella*, is a
phenomenon of very general occurrence.

Among the *Mycetozoa* it was shown by STRASBURGER (44)
to occur in *Trichia fallax* in the developing sporangium, and
later researches (21) have shown that it takes place immediately
before the formation of the spores in this and ten other species
belonging to eight genera.   In three of these (*Craterium*,
Didymium, *Badhamia*), as in *Polystomella*, the protoplasm
becomes aggregated about the dividing nuclei in rounded
masses before the ultimate division into spores.

It appears probable that the phenomenon is akin to the
division of the micro-nucleus which precedes conjugation in the
Infusoria, and to the division of nuclei which occurs in the
maturation of the reproductive elements in the higher forms of
animals and plants.

(b.)   *Orbitolites complanata*.   LAMK.   Figs. 41–51.

My specimens of this species were collected from the reef at
Nukualofa, in Tonga, where it is very abundant.   They were
preserved in 95 per cent. spirit, and have been examined by
means of section.

I have also examined the fine series from Fiji in the Brady
Collection, the property of the University of Cambridge,
and a collection, in spirit, kindly placed at my disposal by
Dr S. J. HICKSON, and obtained by him from the reef at
Talisse Island, to the north of Celebes.

Before I left England my attention was called by the late
Mr H. B. BRADY to this species, which he had obtained from
the reefs of the Fiji Islands, and especially to the desirability of
preserving specimens, with a view to following out their nuclear
history.   The observations recorded in this paper are the out-
come of BRADY's suggestion.

The species is not, however, a good one for throwing light on

the history of the nucleus, as it is so large that each specimen must be examined by means of sections; moreover, the parasitic organisms that it harbours, and the abundance of large food particles contained in the protoplasm, often make it a difficulty to distinguish the nuclear elements proper to the organism itself.

As shown by BRADY (2), the phenomenon of dimorphism is also presented by this species. The individuals fall into two groups, (1) those whose centre is occupied by a "primitive disc" (fig. 45), which consists of the large "primordial chamber" (megalosphere), together with the second or "circumambient" chamber, and (2) those in which the small chambers or chamberlets, as they are called by CARPENTER, are continued to the centre. These evidently correspond with the megalospheric and microspheric forms of *Polystomella* and other Foraminifera.

It will be convenient to deal with the Tongan and Fijian specimens first, and with those from Celebes afterwards.

In the Fijian and Tongan specimens that I have examined there is a marked difference in size between the two forms, the microspheric attaining a much larger size than the megalospheric. Thus, among my thirty-three largest specimens of the megalospheric form from Tonga, the number of rings of small chambers is under thirty in all cases except one, in which it is thirty-eight; among thirteen specimens from Fiji, the greatest number is thirty-three. In the specimens of the microspheric form, on the other hand, the number of rings of chambers varies from 79 to 110, as they are seen in sections of five specimens in the Brady Collection, and I have many examples from Tonga which are equally large.

The shells of this species, as is well known, are bi-concave, being thin at the centre and thick at the margin. As BRADY points out, the central part of the microspheric form, composed, as above stated, of small chambers, is not more than one-third the thickness of the primitive disc which occupies the centre of the megalospheric form.

As the microspheric form increases in size, it frequently happens that the edge of the disc becomes double, so that a

radial section at right angles to the plane of the disc is Y-shaped (fig. 43).

The shells whose margins present this character, and which have only been obtained from Fiji and Tonga, have been separated as a distinct variety, named "*laciniata*" (BRADY). So far as I have seen they are all microspheric.

I may further recall the fact that the peripheral annuli of the full grown disc of this form are often found to be not divided up into small cubical or columnar chambers, as are those lying nearer the centre, but are composed of spacious chambers extending vertically through the whole thickness of the disc, and circumferentially round a considerable portion of its circuit.   These may be called the *brood chambers* (fig. 43). In specimens which BRADY obtained from the reefs of Fiji these chambers contained multitudes of young shells, consisting of the "primitive discs" of the megalospheric form.

I have now to give the results of my examination of preserved specimens.

MICROSPHERIC FORM.—All the examples of this form which I have examined, were full grown or nearly so. As above stated, the central part of the shell is occupied by small chambers.   I have not been able to distinguish the central chamber (microsphere) from those which surround it, in the preparations I have seen.

Before the young are formed, the protoplasm fills all the chambers of the disc, with the exception of the brood chambers, which contain only a thin lining of protoplasm. This may in part be due to the withdrawal of the protoplasm as the result of the action of the spirit.

In the specimens of which I have cut sections (fourteen), numbers of small rounded nuclei are thickly scattered through the protoplasm, so that two or more often appear in the section of a single chamber (fig. 41).   The great majority of these are about 6 to 10 μ in diameter, but some reach 20 μ.

A reticular structure may often be seen in the nuclei, and small darkly-stained masses, which appear to be nucleoli, are seen near the peripheral parts of the nucleus.   The smaller

nuclei are very often disposed in pairs in the protoplasm, and in some cases the pairs may be seen to be united by a constricted band, being killed in process of division (fig. 41). The nucleoli in such dividing nuclei are as distinctly seen as in those which are single.

There appear to be all intermediate forms between the small nuclei and the larger ones. In the latter the reticulum is more clearly seen, and the nucleoli are less conspicuous. They are, moreover, not disposed in pairs, but solitary (fig. 42).

There are generally numbers of stained particles present in the protoplasm, some of which appear to be food material. It is possible that others may be of nuclear nature, but I have not recognised in these specimens anything of the nature of the stained strands met with in the microspheric form of *Polystomella*.

Reproductive Phase.—I have met with thirteen specimens among my preserved material, in which the brood chambers contained young. In those which have been decalcified (seven), the part of the disc internal to the brood chambers contained no protoplasm. It is clear that the protoplasm has been withdrawn from the small chambers of the disc and massed in the brood chambers, where it has been divided up into the young. In such specimens this central part is quite transparent, and consists of the organic basis of the walls of the chambers, together with the larger parasitic algæ which are contained in them (fig. 43).

In marked contrast to the central region are the brood chambers at the periphery, closely packed with the young (figs. 43 and 44). In all my specimens the young are fully developed, and in all they belong to the megalospheric form. They consist of the primordial and circumambient chambers, invested by the darkly staining basis of the thin shell, from which the calcareous salts have been dissolved. The protoplasm of the primordial chamber is generally denser, and takes a darker stain than that in the circumambient chamber, and an oval nucleus measuring about $20 \times 15 \mu$ lies in it. Even in this young condition the small parasitic algæ are present in the protoplasm.

As in BRADY's specimens, the young shells are set in the brood
chambers, with their plane at right angles to that of the portion
of the disc which contains them.   Fig. 43 represents a vertical
radial section through a disc containing young, and fig. 44 a
vertical tangential section of such a disc.   It will be seen that
a considerable amount of protoplasm is present in the brood
chambers, filling in the interstices between the young shells.
This generally contains great numbers of the small algæ, but I
have failed to find any nuclei in it.   It is, no doubt, continuous
through the pores of the shells with the protoplasm of the
young.

When the central region of the disc is thus left empty, the
large parasitic algæ contained in it, which are too large to pass
through the channels connecting the chamberlets with one
another, are found in active division, their reproductive phase
following that of their host.

This species is often found attached to the green ovate
leaves of a plant which grows in the shallow water on the reef.
On one occasion when I had brought in some large specimens
and put them with the leaves in a dish of water, in the course
of a few hours I found numbers of the megalospheric young
which had escaped from a shell and lay scattered over the
leaves and the surface of the parent, whose large brood chambers
were empty.

The large shells lie flat on the leaves, but the young ones
with few rings of chamberlets or none, often cruise about on
the edge of the disc, which is thus directed vertically to the
supporting object.   Sometimes, when the specimens were kept
in dishes, the young shells were found floating at the surface
of the water with a film of pseudopodia extended about them,
in the same manner as pond snails often float supported by a
raft of mucus.

THE MEGALOSPHERIC FORM.—As stated above, the megalo-
spheric form begins its existence with a single nucleus situated
in the primordial chamber (figs. 46–48).   This nucleus main-
tains its position during a greater part of the period of growth.
Thus among thirty-one examples of the megalospheric form in

which the rings of chamberlets numbered from seventeen to thirty-eight, there are eighteen whose primordial chamber still contains a single nucleus. The nucleus measures about $24 \times 14 \mu$, it is of a round or oval shape, and a close reticulum can be detected in the interior. I have not seen definite nucleoli, but the central region of the nucleus often appears, in sections, to be separated from the peripheral region by a ring of more deeply stained particles (figs. 47 and 48).

In one specimen, with twenty-two rings of chamberlets, two rounded nuclei are present in the primordial chamber. In several others (fig. 49) no nucleus of the form above described is to be seen, but in its place, numbers of compact bodies of different sizes, and often of irregular shape, are present. These are not confined to the primordial chamber, but extend into the circumambient chamber and surrounding chamberlets. It would appear that in the megalospheric form of this species, after the individual has nearly completed its growth the nucleus breaks up into a number of fragments, which become dispersed among the chambers.

Dr Hickson's collection from Celebes consisted of 117 specimens. They were obtained from the reef at Talisse Island, to the north of the main island. Although, in this species, the central chambers are not covered by those that are added later, they are frequently obscured by a calcareous deposit on the surface. By dissolving the superficial parts of the shell, the central chambers may be exposed and their character recognised. In some cases, however, the central chambers are empty, and their character can then only be observed by examining the delicate organic basis of their walls. I failed to recognise the character of the central chambers in two cases, but of the remaining specimens only one belonged to the microspheric form, the others being megalospheric. The size attained by shells of the megalospheric form is much larger than in those which I have seen from Fiji or Tonga. In one case there are as many as sixty-six rings of chamberlets between the primitive disc and the periphery. In sections of

these specimens numbers of rounded bodies, which appear to
be nuclei, can be detected in the protoplasm.

In three examples of the megalospheric form, while the
central chambers of the shell are empty, those at the periphery
have the form of brood chambers, and are crowded with young
" primitive discs," similar to that whose empty chambers occupy
the centre of the parent shell (figs. 50 and 51).

The young are disposed in the brood chambers in the same
way as in the microspheric forms from Tonga and Fiji, above
described, except that, owing to the thinness of the margin of
the disc, as compared with these specimens, the young in each
annulus are in a single row. I have failed to recognise a
nucleus in the young form, probably owing to the imperfect
preservation. The specimens containing young belong to a
batch collected in the month of November.

We are here then brought face to face with the fact that in
this species megalospheric young are produced by megalospheric
parents, while it is no less certain that (in Fijian specimens, as
described by Brady, and in Tongan specimens, as I have shown)
megalospheric young are produced by microspheric parents.
The relation of the two forms to one another will be discussed
at the end of this paper*.

It may be pointed out here that, in the Tongan specimens,
the nuclear characters of the two forms agree fairly well with
those of *Polystomella*.

In the microspheric form numbers of rounded nuclei are
found scattered through the protoplasm, and they may be found
in process of simple division. I have not, however, recognised
anything like the giving off of deeply staining strands, which is
so marked a feature in *Polystomella*.

In the megalospheric form, a single nucleus is found during
a large part of the growth of the individual, and ultimately it
appears to break up into a number of fragments.

In *Polystomella*, as we have seen, the nucleus of the me-
galospheric form increases in size with the growth of the

protoplasm. In *Orbitolites*, however, the nucleus in the pri-
mordial chamber is hardly larger in the examples with many
rings of chambers than in those with few.

The Celebean specimens are in a phase of growth to which
I have found no analogy in *Polystomella*.

The account of the nuclei of *Orbitolites* here given differs
from that of Professor BÜTSCHLI in which numbers of minute
and irregular nuclei are described scattered through the proto-
plasm. Possibly his examination was confined to such later
stages of megalospheric specimens as those which I obtained
from Tonga, in which, as above described, the nuclei are found
in this condition.

(c.) *Rotalia Beccarii* (LINN.). Figs. 38–40.

Among seven examples of this species, six were megalo-
spheric, and one microspheric.

MICROSPHERIC FORM. In the representative of this form
there are thirty-two chambers. The microsphere measures $13\,\mu$
in diameter (fig. 38). Some twenty-four nuclei are present,
irregularly distributed through chambers 10 to 25. As in
Polystomella, the nuclei increase in size from within outwards.
I see no "stained strands," but the protoplasm of the imme-
diate neighbourhood of some of the nuclei has taken a diffused
flush[*].

MEGALOSPHERIC FORM (fig. 39). The mean diameter of the
megalosphere varies between 37 and $65\,\mu$, having an average of
$54\cdot6\,\mu$. In the four cases in which the protoplasm is preserved,
a single large nucleus is present, situated some distance behind
the middle point of the protoplasm. In one case it is drawn
out into the succeeding chamber, in the other three whose nuclei
are round or oval, the mean diameter of the nucleus varies
between $27\cdot5$ and $33\,\mu$. In each case fairly large nucleoli are
present (fig. 40).

[*] As stated in Postscript 2, I have observed the production of megalospheric
young by a microspheric parent in this species.

(d.)   *Truncatulina lobatula* (W. and J.).

When the shells of this species are decalcified, a brown and apparently chitinous element remains, which retains the size and shape of the chambers.   This is present in the walls of the inner chambers of many species, but is particularly well developed in this.

In a single example of the *Microspheric* form, the microsphere measures $11 \times 10 \mu$, and at least seven nuclei are present.

In twelve examples of the *Megalospheric* form, the mean diameter of the megalosphere varies between 35·5 and 15μ, and has an average of 28μ.   In the three cases in which the protoplasmic contents are preserved (including the example with the megalosphere of 15μ diameter), a single large nucleus is present.

Eight examples from Tonga appear to belong to BRADY'S species, *T. tenuimargo*.   They are all of the megalospheric form, the mean diameter of the megalosphere varying between 24 and $14\cdot5 \mu$, and having an average of $20\cdot8 \mu$.   In five specimens which contain protoplasm (including that with the megalosphere of $14\ 5 \mu$) a single large nucleus is present.

Thus, in *Truncatulina*, the diameter of the megalosphere, though often considerable, may be so small as to approach that of the microsphere.   In these cases, if the size of the central chamber were the only character on which to rely, it would be doubtful to which form the specimen should be referred.   It appears, however, that this is indicated by the character of the nuclei.   In the example of the microspheric form, whose central chamber measures $11 \times 10 \mu$, at least seven nuclei are present, while the specimen of the megalospheric form whose central chamber is smallest ($14\cdot5 \mu$) has a single large nucleus measuring $20 \times 15 \mu$.

(e.) *Calcarina hispida*, BRADY. Figs. 34–37.

Some examples of this species were contained in sand collected with corals from a depth of from 20 to 40 fathoms off the Tonga Islands. They were preserved in spirit of about 70 per cent. Of these, twenty-two belong to the megalospheric form, and two to the microspheric. In this species also there is a considerable quantity of the chitinous element in the walls of the chambers, which remains after the lime has been dissolved. Owing to the presence of this substance the walls of the chambers of specimens which are mounted in Canada balsam are generally to some extent shrivelled; hence the measurements of the chambers fall rather short of their proper size.

The average mean diameter of the megalosphere in twelve specimens is 49 μ, the extremes being 58·5 and 38·5 μ (fig. 34).

The microspheres in the two microspheric examples measure 15 × 12·5 μ and 13 × 11 μ (fig. 35).

In the thirteen examples of the megalospheric forms in which the preservation is sufficiently good to show the nuclear characters, a single large nucleus is present (fig. 34).

In one of the microspheric forms at least five small nuclei can be seen, and probably others are present, but the preservation is not sufficiently good to allow the nuclei to be well seen.

In the other microspheric specimen, while the inner chambers are empty, several of the terminal chambers contain numbers of large protoplasmic bodies, in number about 140 (figs. 36 and 37). At first these bodies are flattened against one another, but as the series of chambers is followed they assume a more perfectly oval shape. In seven examples the mean of the long and short diameters is 58·3 μ. A round nucleus may be detected in many of them.

It appears probable that these bodies are young megalospheric individuals which have not yet acquired a shell.

(f.) Cycloclypeus Carpenteri, BRADY.   Figs. 52-54.

I obtained a few examples of this rare species to the south-east of Nomuka, in the Tonga Islands, at a depth of from 20 to 40 fathoms.

On decalcifying them two were found to have been preserved with the protoplasm contained in the shell. One of these, which measured about 1 centim. in diameter, was mounted whole, after staining with picro-carmine, and sections were cut of the other (which was smaller) parallel to the plane of the disc.

In both specimens large chambers, resembling to some extent the primitive disc of *Orbitolites complanata,* LAMK., occupy the centre of the shell (fig. 52). These consist of: (1) A somewhat oval chamber which appears to be the megalo-sphere, measuring 300 × 205 μ. (Owing to the shrivelled condition of the walls of the inner chambers, which consist of a thin apparently chitinous layer, these numbers are only approximately correct.) (2) A very large crescent-shaped chamber, in the concave side of which the megalosphere lies. The length in a straight line is 610 μ, and the greatest breadth 310 μ. In the sections a single short canal can be detected passing from the megalosphere to the second chamber, at about the middle of the concave side. (3) Another somewhat crescent-shaped chamber, enclosing the other side of the megalosphere; while its length is about equal to that of the second chamber, its breadth is very much less (under 100 μ). This chamber appears to be intermediate in character between the large chambers and the small ones making up the surrounding annuli.

The two crescent-shaped chambers thus surround the megalosphere. Their ends are in apposition, the third chamber somewhat overlapping the second on the outer side, and they communicate at either end by short canals passing from one chamber to another.

The first ring of chambers surrounds these three, communicating with the crescentic chambers by several short canals,

and the others follow in concentric rings, but the innermost ring is less completely divided up into cubical chambers than those which follow.

As in the megalospheric forms described above, a large nucleus is present. In the large specimen it lies in the second chamber (fig. 52), and is nearly spherical, measuring about 85 μ in diameter. In the other, of which sections were cut, it lies in the megalosphere, and has an oval shape, measuring 60 × 40 μ. In section (fig. 54) it presents the appearance of a close reticulum with dark masses of different sizes embedded in it, and is surrounded by a dark line which clearly separates the nucleus from the coarse reticulum of the protoplasm. This obscure structure of the nucleus is no doubt due to the imperfect preservation.

3. Concluding Remarks.

From the evidence now presented, it appears that the following statements relating to the life-history of the Foraminifera may be accepted.

1. The species of Foraminifera are in a great number of cases dimorphic. Relying on the difference in size of the central chambers of the shells, the dimorphism has been stated to exist in four out of the ten families into which BRADY divided the group. This is shown in the following table:—

Family.	Authority.	Reference. (The numbers refer to the works named at the end.)
I. Gromidæ.		
II. Miliolidæ.		
Sub-Fam. Miliolinæ.		
Biloculina		
Dillina		
Fabularia		
Lacazina		
Triloculina . . .	MUNIER-CHALMAS and SCHLUMBERGER	25
Trillina		
Quinqueloculina . .		
Pentellina		
Heterillina . . .		
Spiroloculina	SCHLUMBERGER . . .	36
Adelosina	SCHLUMBERGER . . .	35
Sub-Fam. Peneroplidinæ.		
Orbitolites	BRADY	2
Sub-Fam. Alveolininæ.		
Alveolina	MUNIER-CHALMAS, fide SCHLUMBERGER	33
III. Astrorhizidæ.		
IV. Lituolidæ.		
V. Textularidæ.		
VI. Chilostomellidæ.		
VII. Lagenidæ.		
Sub-Fam. Lageninæ.		
Nodosaria	SCHLUMBERGER . . .	33
Dentalina		
Sub-Fam. Polymorphinæ.		
Siphogenerina . . .	SCHLUMBERGER . . .	33
VIII. Globigerinidæ.		
IX. Rotalidæ.		
Sub-Fam. Rotalinæ.		
Rotalia	SCHLUMBERGER; L.* .	33
Truncatulina	L.	
Calcarina	L.	
X. Nummulinidæ.		
Sub-Fam. Polystomellinæ.		
Polystomella	L.	
Sub-Fam. Nummulilinæ.		
Amphistegina . . .	SCHLUMBERGER . . .	33
Nummulites . . .	MUNIER-CHALMAS . .	24
Assilina		

2. The two forms differ from one another in the following features :—

(a) The size of the central chamber.

From their difference in this respect the two forms are

* The observation is my own.

distinguished as *Megalospheric* and *Microspheric*. The contrast in size between the megalosphere and microsphere is much greater in some species than in others.

In *Biloculina depressa*, D'ORB., according to SCHLUMBERGER, the diameter of the megalosphere is between 200 and 400 μ, while the mean diameter of the microsphere is 20 μ.

In *Polystomella crispa* (LINN.), the megalosphere varies, in the specimens in which I have measured it, from 165 to 35 μ in diameter, and the microsphere from 13 to 6·5 μ.

In *Rotalia Beccarii* (LINN.), the difference is less. Among five examples of the megalospheric form the diameter of the megalosphere varied from 65 to 37 μ; the diameter of the microsphere in one individual was 13 μ.

In the allied form, *Calcarina hispida*, BRADY, among the twelve examples the diameter of the megalosphere varied from 58 to 42 μ, and that of the microsphere in two examples from 14 to 12 μ[*].

In the description above given of *Truncatulina*, it was shown that, while the megalosphere is usually considerably larger than the microsphere, it may approach it closely in size. Possibly there are genera of Foraminifera in which the central chambers of the two forms are of the same size. In such cases, analogy with the types above described would lead us to look for differences in the nuclei by which they might be distinguished. It cannot however be assumed that all forms of Foraminifera are dimorphic.

(*b*) The shape and mode of growth of the chambers succeeding the megalosphere and microsphere.

SCHLUMBERGER has called attention to the very interesting fact, that in many species among the Miliolidæ the chambers immediately succeeding the central one are arranged on the biloculine plan in the megalospheric form, and on the quinqueloculine plan in the microspheric form (woodcut, p. 114.)

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[*] The numbers given are not strictly comparable in the different species, for while, in *Biloculina*, the measurements are taken from sections of the shell, in the others they are from decalcified and mounted, and hence somewhat shrunken, specimens.

In several species the second chamber of the megalospheric form is peculiar. Thus, in *Orbitolites*, it forms the large circumambient chamber (CARPENTER) which almost surrounds the primordial chamber (megalosphere); in *Cycloclypeus* the second chamber has a similar relation to the megalosphere. In *Polystomella* it is not so large in proportion as in these forms, but it is applied to the megalosphere for the whole of its length. In other species the second chamber differs little in shape from those which follow it.

The size attained by the complete shell is, in some species, markedly different in the two forms, while in other species this difference does not exist.

In *Nummulites* the microspheric form grows to a much larger size than the megalospheric. In *Polystomella*, however, the two forms attain about the same size.

Among the Miliolidæ, according to SCHLUMBERGER, the microspheric form is usually the larger, but in *Adelosina polygonia*, SCHLUMBERGER, the megalospheric form attains a rather larger size than the microspheric (1·5 to 1·4 millim.).

(c)   The character of the nuclei.

In *Polystomella crispa* (LINN.) it has been shown that in the megalospheric form a single large nucleus is present during the greater part of the life of the individual, while in the microspheric form numbers of smaller nuclei are found. How far this contrast in the nuclei in the two forms is of general occurrence among the Foraminifera remains to be seen. In *Rotalia Beccarii* (LINN.), and *Calcarina hispida* (BRADY), in which I have seen the nuclei of both forms, the condition was similar to that found in *Polystomella*, the megalospheric form having a single large nucleus, the microspheric form several small ones.

In *Cycloclypeus*, in which I have only seen two megalospheric forms, a single large nucleus was present.

In *Orbitolites* the conditions of the nuclei found in the two forms are, on the whole, similar, but a phase is here presented, the production of megalospheric young by megalospheric parents, of which I have no evidence in *Polystomella*.

3. The two forms differ in the frequency of their occurrence, the megalospheric form being much more abundant than the microspheric.

In *Polystomella crispa* (LINN.), among the examples that I have seen, the proportion of the megalospheric forms to microspheric is as 34 to 1*. In *Adelosina polygonia*, SCHLUMBERGER gives the relative proportions of the two forms as 8 to 1.

4. The megalospheric form arises as a young individual already invested by a shell, which may be found lying in or about the peripheral chambers of the parent. Such megalospheric young have been seen in—

; *Miliolinæ*, by GERVAIS (12), M. SCHULTZE (38), SCHLUMBERGER (32), and SCHNEIDER (37).

Peneroplis proteus, D'ORB., by SCHACKO (29).

Orbitolites, simple form, by SEMPER (43).

    „   *complanata*, LAMK., by LISTER.

    „   *complanata*, var. *laciniata*, BRADY, by PARKER, CARPENTER, BRADY (2), and LISTER.

Spirillina vivipara, EHRB., by EHRENBERG (11), and STRETHILL WRIGHT (45).

Cristellaria crepidula (FICHTEL and MOLL), by BRADY (1).

Rotalina, sp., by M. SCHULTZE (40).

Calcarina hispida, BRADY, by LISTER.

Megalospheric young may be produced both by microspheric and megalospheric parents.

In the specimens of *Orbitolites complanata*, var. *laciniata*, described by BRADY, and in those which I have examined, the parents of such young are microspheric.

. In MAX SCHULTZE'S account of the production of young by one of the Miliolidæ, it is stated that the parent was distinguished from other individuals in the aquarium by its large size. As it is generally the case in this family that the microspheric form attains a larger size than the megalospheric, it is probable that in this case also the parent was microspheric.

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* Among specimens collected in July and August, 1894, the microspheric forms were, however, more abundant than here indicated.

The specimen of *Calcarina hispida*, BRADY, described above, was microspheric, and here, too, the young were probably megalospheric*.

On the other hand the production of megalospheric young by megalospheric parents has been seen in several instances.

In the specimens of *Orbitolites complanata*, LAMK., from Celebes, described above (figs. 50 and 51), megalospheric parents are giving rise to megalospheric young.

In SCHACKO'S specimen of *Peneroplis proteus*, D'ORB., the central chambers of the young and of the parent were of the same size, measuring about 35 μ in long diameter. It seems probable that they were both megalospheric.

MAX SCHULTZE'S *Rotalia* is said to have had a central chamber of the same size as those of the young which it produced. The diameters of these varied from 25 to 34 μ. Judging by the size of the megalosphere (37–65 μ) and microsphere (13 μ) in *R. Beccarii* (LINN.), it appears probable that this was a megalospheric individual producing megalospheric young.

Again, in the specimen of *Cristellaria crepidula* (FICHT. und MOLL.) figured by BRADY, the first chamber of the parent shell measured 110 μ × 84 μ, while those of the contained young varied from 60 to 30 μ. It seems clear that the parent, at any rate, was megalospheric; the nature of the young shells is less evident, but the range of variation between the size of the parent shell and that of the smallest young is not greater than that recorded above in the size of the megalosphere among different examples of *Polystomella*, so that it is not impossible to regard them as megalospheric also.

5. Under certain circumstances active zoospores are produced by Foraminifera.

These have been recorded by STRETHILL WRIGHT in *Gromia*, and by MURRAY in *Cymbalopora* (in specimens with the large inflated chambers).

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* To these instances have now to be added *Polystomella crispa* (LINN.) and *Rotalia Beccarii* (LINN.), as recorded in Postscript 2.

A specimen of the megalospheric form of *Polystomella crispa* (LINN.) is described above whose protoplasm was broken up into small round spores of uniform size, and I have seen such uniform spores escape from the broken shell of a specimen. The *Euglena*-like bodies, described by SCHNEIDER (37), may possibly have been of the same nature.

When the existence of dimorphism in the species of Foraminifera was brought forward by MUNIER-CHALMAS, it was, as we have seen, supposed that the microspheric form was a modification of the megalospheric. It was suggested that when the megalospheric form attained a certain size an absorption of the central chamber occurred in some individuals, the space which it had occupied being then filled in by small chambers, while additional chambers were added at the outside of the shell. Small megalospheric forms would thus be converted into the large microspheric forms.

DE HANTKEN and DE LA HARPE (15), and more recently, VAN DEN BROECK (5), have brought forward strong reasons for rejecting the hypothesis that the microspheric form is produced by modification of the megalospheric.

In the genus *Biloculina* among the Miliolidæ, as SCHLUM-BERGER has shown, the plan of growth of the chambers immediately succeeding the central chamber differs entirely in the two forms (*cf.* the woodcut on p. 114), and this difference produces an effect on the form of the ultimate chambers. As in the case of the two forms of the Nummulites cited by DE HANTKEN and DE LA HARPE the hypothesis would imply a remodelling of the whole shell. Again, in the bi-concave discs of *Orbitolites* the centre of a megalospheric individual is three times as thick as that of a microspheric. Hence to convert the megalospheric form into the microspheric, not only the primitive disc but many of the inner rings of chamberlets must be absorbed and replaced by fresh ones.

If such a process were to occur, the replacement of the chambers would not take place very rapidly, and various stages should be found. Such stages are, however, not found.

While the megalospheric form is not found in process of transition into the microspheric, it has been found either with the protoplasm broken up into zoospores (*Polystomella*), or containing megalospheric young in the peripheral chambers, while the central chambers are empty (*Orbitolites*, &c.). In both cases the megalosphere remains unabsorbed at the centre of the shell.

The microspheric form is met with in the young stage (fig. 7), though such specimens are necessarily rare, owing to the small numbers of the microspheric form as compared with the megalospheric.

The nuclear characters of the two forms are, in the species at any rate which I have examined, quite distinct.

It appears that we may safely conclude that the microspheric and megalospheric forms are distinct from their origin.

What then is their relationship ?

When two forms of a species are met with in animals or plants they generally either belong to different sexes or they are members of a cycle of recurring generations.

The hypothesis that the two forms of the Foraminifera represent the two sexes appears to be disproved by the fact that in *Orbitolites complanata*, LAMK., both megalospheric and microspheric forms are found with the young of the megalospheric form (primitive discs) in their brood chambers. Other genera furnish analogous, though less complete evidence. Hence it is impossible to regard either form as male.

We turn then to the other hypothesis, namely, that the two forms are members of a recurring cycle of generations.

[This view receives further support from the facts that in the reproduction of the microspheric form (Postscript 2) the whole of the protoplasm of the parent is divided into the young, and that these all belong to one form, the megalo-

spheric. On the hypothesis that the two forms represent different sexes, we should expect to find both megalospheric and microspheric young produced by the microspheric parent.

Adopting this view, the individuals of the microspheric generation of *Polystomella* give rise asexually, by a process of multiple fission, to young megalospheric forms, and these in their turn produce, also by multiple fission, the flagellate zoospores.

In *Orbitolites* the microspheric form gives rise to megalospheric young, but in this genus, as in *Peneroplis* and *Rotalia*, the megalospheric form may repeat itself for one or more generations, though ultimately it may be assumed by analogy with *Polystomella*, that a megalospheric form is produced which gives rise to zoospores.

How is the gap in the life-history between the liberation of the zoospores and the formation of the microsphere filled in ?

SCHAUDINN has recently described (*Sitz-Ber. Gesellsch. Naturforsch. Freunde*, Berlin, Jahrg. 1894. Abstract in 'Zool. Centralblatt,' I, p. 519) the production of zoospores of approximately uniform size, in *Hyalopus* (*Gromia dujardinii*, M. SCH.) and their subsequent conjugation.

It appears not improbable that a similar process may occur in *Polystomella* and the other dimorphic species, the initial chamber of the microspheric form being the result of the conjugation of zoospores of the megalospheric form. The sizes of the zoospores and microsphere in *Polystomella* (about 4μ and 6–13μ, respectively) accord fairly well with this view; and the comparative scarcity of the microspheric form may be understood on the supposition that the union of two separate organisms is required for its production.

If this is the case, the two forms of the Foraminifera must be regarded as sexual and asexual generations, of which the sexual generation retains the power in some genera (*Orbitolites* and others) of reproducing asexually.

It must, however, be borne in mind that while there seems good reason to regard the two forms of Foraminifera as belonging to different generations, the view above suggested of the

sexual nature of the zoospores of the megalospheric form is at present insecure. There is no direct evidence of the conjugation of zoospores or the mode of origin of the microspheric form in a dimorphic species.]

POSTSCRIPT 1.

In reviewing the previous work on the life-history and nuclei of the Foraminifera, I have confined myself to a rather limited range of forms. I have done so because it appeared best to select the evidence of such forms as are most obviously related to those which I had to describe.

SCHAUDINN has recently published (31) a preliminary account of his researches into the reproduction and mode of increase of the nuclei in the Foraminifera. This I did not see until after my paper was written. Many of the observations appear to be of the highest interest, but no mention is made of the important fact of the existence of dimorphism. *Polystomella crispa* (LINN.) is described as usually having one or four nuclei, but is said to become many-nucleated during reproduction; a form of reproduction is also described in which the whole of the protoplasm leaves the shell and divides up into numbers of young individuals which assume the characteristic shape of the species. SCHAUDINN has, however, apparently failed to recognise what is undoubtedly the fact, that in this species one in every thirty to forty individuals is microspheric and possesses nuclei of a quite different character from that of the megalospheric form.

In his account of the changes which the nuclei of the Foraminifera undergo preparatory to reproduction, SCHAUDINN describes a breaking up of the nucleus into fragments which are dispersed through the protoplasm; in this general result, my observations on the nucleus of the megalospheric form of *Polystomella*, so far as they go, agree with his, but I am quite unable to recognise the remarkable phases of the process which he describes in those that I have seen.

POSTSCRIPT 2. AUGUST 3, 1894.

It is stated above that I had no evidence as to the fate of the microspheric form of *Polystomella crispa* (LINN.).

I have since made further observations on living Foraminifera (chiefly *Polystomella*), and have seen in some hundreds of cases the mode of reproduction mentioned by SCHAUDINN.

The specimen of *Polystomella*, as seen attached to the glass walls of a vessel, becomes surrounded by a halo of closely-set radiating pseudopodia. After some hours the protoplasm is withdrawn from the shell, emerging into the area covered by the halo. Here, after involved streaming movements, it gradually divides into distinct spherical masses, which, in the case of the specimens in my jars, usually had a diameter of 50 to 60 μ.

In a short time these masses secrete a shell, and, some four or five hours after they first became distinct, they throw out long pseudopodia, and rapidly draw apart from one another and from the empty parent shell. In the course of a few hours the wall of a second chamber is formed, a third and fourth being added by the second day after separation occurred. In this stage they are readily recognized as young megalospheric individuals.

After the protoplasm has left the central part of the shell there is no direct evidence, in decalcified specimens, as to the nature of the parent; but in specimens (some fifty or more) killed and decalcified at earlier stages of the reproductive process it is seen that the parent is in every case microspheric.

The fate of the microspheric form of *Polystomella crispa* (LINN.) is, then, to give rise to megalospheric young.

In two examples of *Rotalia Beccarii* (LINN.) the same process occurred. The parent in each case was microspheric.

The fact that the whole of the protoplasm of the parent is used in the production of the young, and that these are all of one form, supports the view that the two forms of the Foraminifera belong to different generations.

A fuller account of the process of reproduction, with what I am able to make out of the nuclear changes, will be reserved for another paper.

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DESCRIPTION OF PLATES.

List of Reference Letters.

b. Brown bodies.
c. Spiral canal in the umbilical region of the shell.
f. Foreign particles.
M. Megalosphere.
m. Microsphere.
N. Nucleus.
s. Bodies in the protoplasm, staining red with picro-carmine, and
       here regarded as nutritive in nature.
st. Stained strands.
v. Vacuole.

Figs. 1 to 33, with the exception of 4, a and b, relate to *Polystomella crispa* (LINN.).

Fig. 1.   × 230.   Part of a megalospheric specimen in which the nucleus has been involved in a movement of the protoplasm, probably the effect of the reagent.   N. The main mass of the nucleus.   N'. Portions of the nucleus carried on by a movement of the protoplasm.   Sublimate and picro-carmine.

Fig. 2.   × 250.   Example of a megalospheric individual in which the protoplasm contains numbers of spherical bodies (s), probably nutritive, which take a red stain in picro-carmine.

Fig. 3.   × 523.   End of one of the chambers of a similar specimen.

Fig. 4a.   × 690.   *Balantidium entozoon* (EHR.).   Specimen containing numbers of darkly staining spherical bodies, probably nutritive.

Fig. 4b.   × 1460.   One of the spherical bodies from another specimen of *Balantidium entozoon*.   Osmic vapour, picro-carmine.

Fig. 5.   × 1047.   End of a chamber of a specimen containing brown bodies (b).

Microspheric form.

Fig. 6a.   × 170.   Complete specimen, with forty-two* chambers.   As the series of chambers is followed towards the centre, the nuclei lose their rounded shape, and strands of nuclear substance are seen scattered through the protoplasm.

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* This is the number of chambers of whose presence there are indications in the decalcified specimen.   It frequently occurs that in the live state one or more of the terminal chambers contain little or no protoplasm, and hence might not be represented after decalcification.   The same remark applies to the other descriptions in which the number of chambers is given.

Fig. 6 b
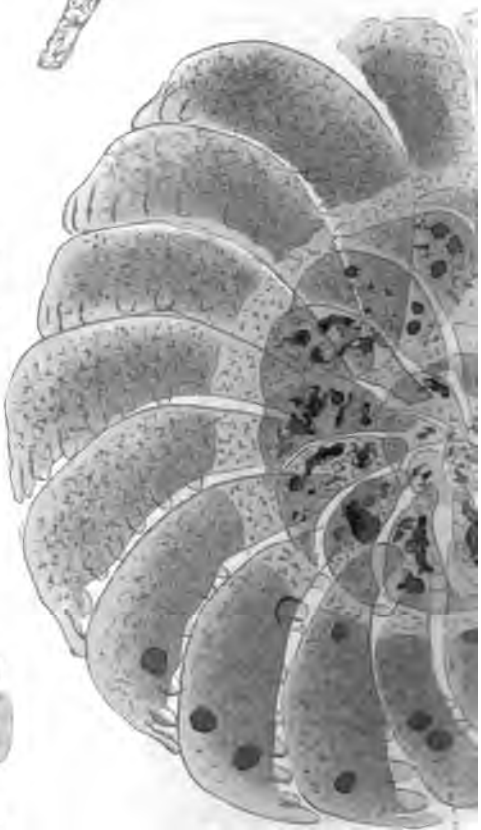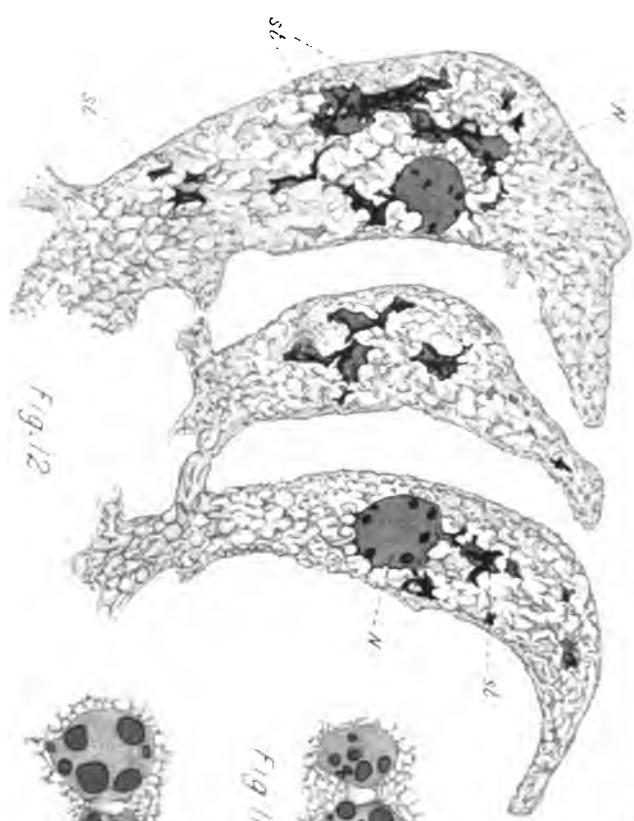
Fig. 12

Fig. 11 b

Fig. 11 a

Fig. 11 c

Fig. 6 a

Fig. 8 b

Fig. 8 a

Fig. 9

Fig. 10
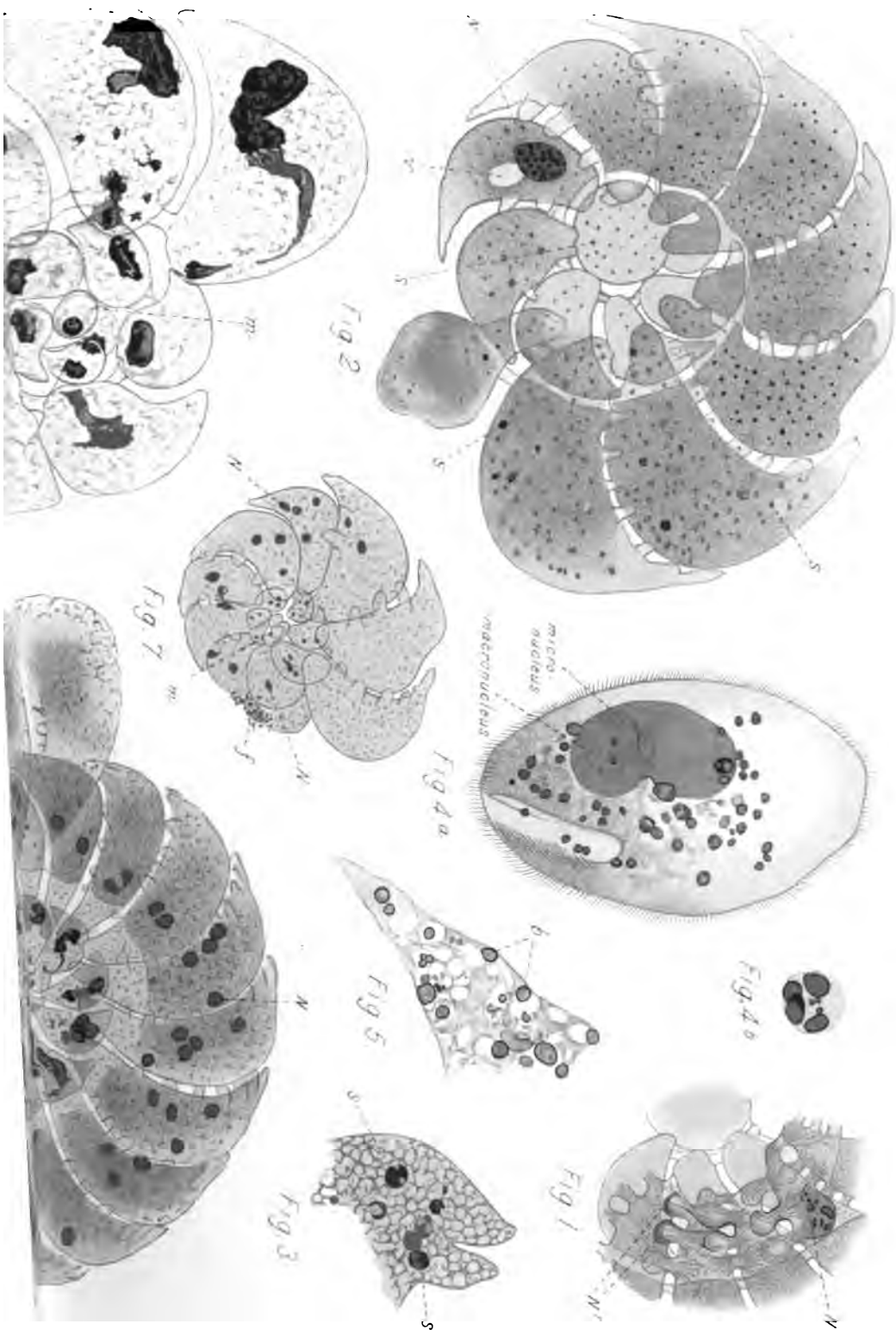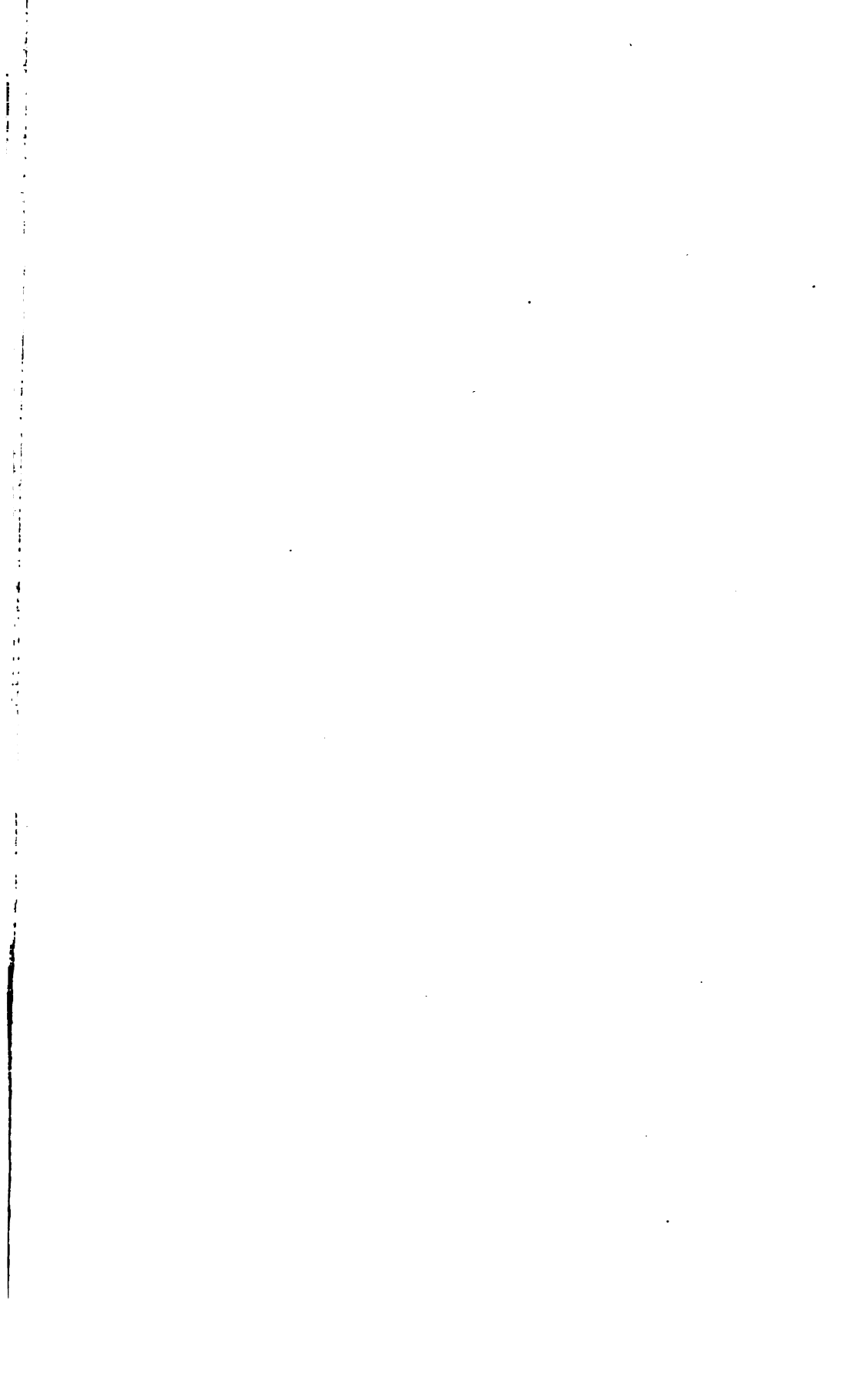
Fig.24.
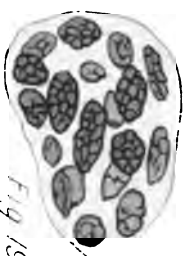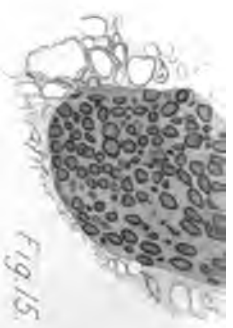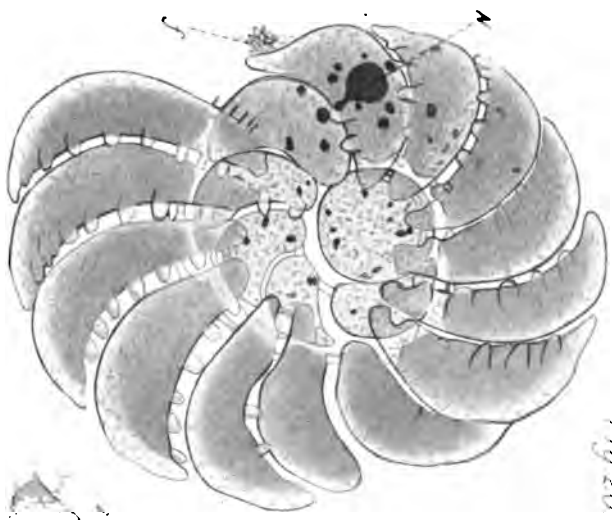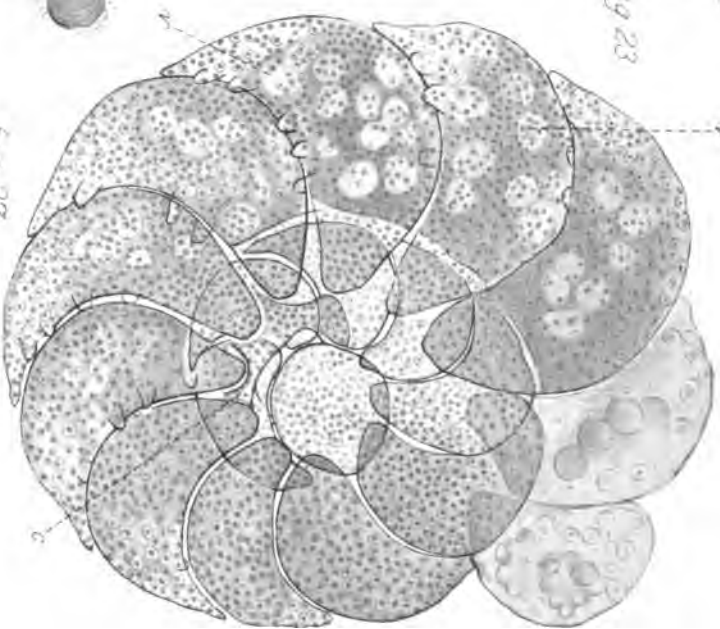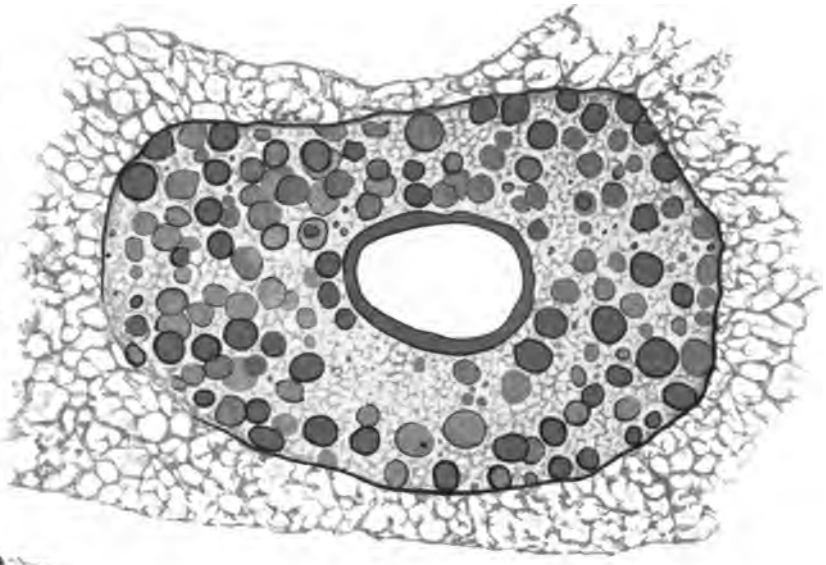
Fig 17

Fig 19

Fig 19

Fig 20

Fig.25

Fig.26

Fig 21

Fig 23

Fig 27

Fig 16

Fig 15

Fig 14

Fig.22

Fig 13

between chambers

canals

retral process

Fig. 33a.

Fig. 40

Fig. 37

Fig. 39

Fig. 35

Fig. 34

Fig. 38

Fig. 36

Fig. 32b

Fig. 32a

N

f

f

N

J. J. Lister del

Fig. 50

P.D

Fig. 51 c

algae

Fig. 54

Fig. 53
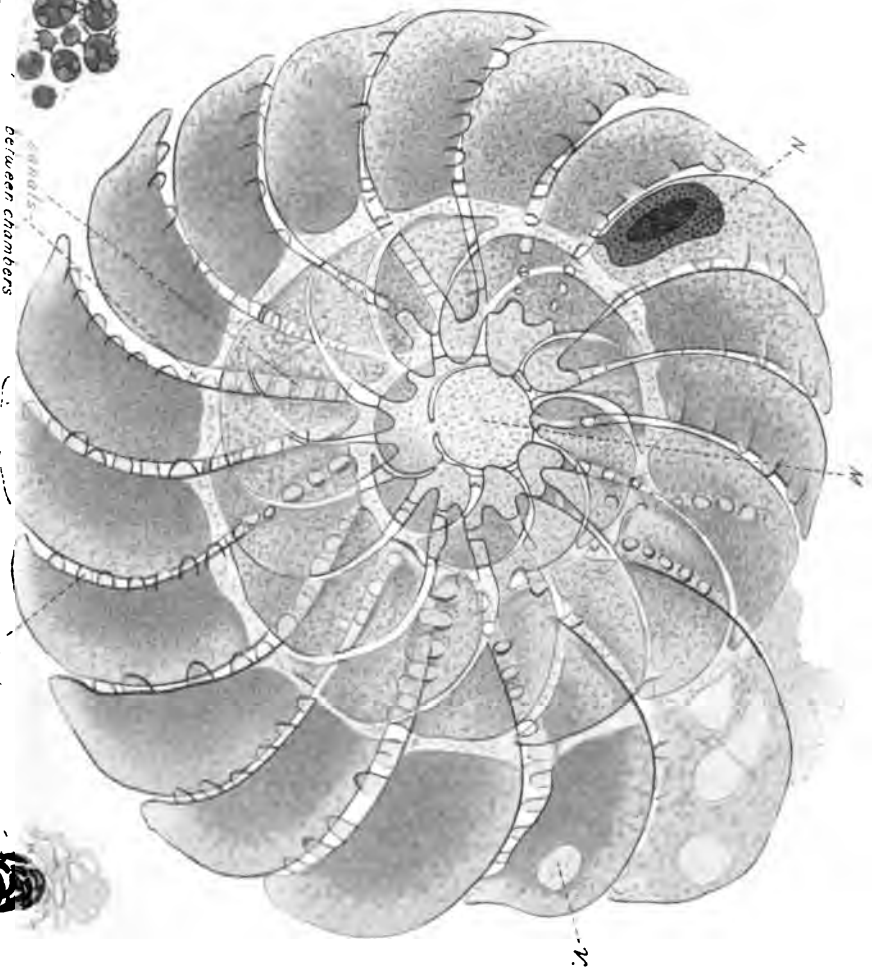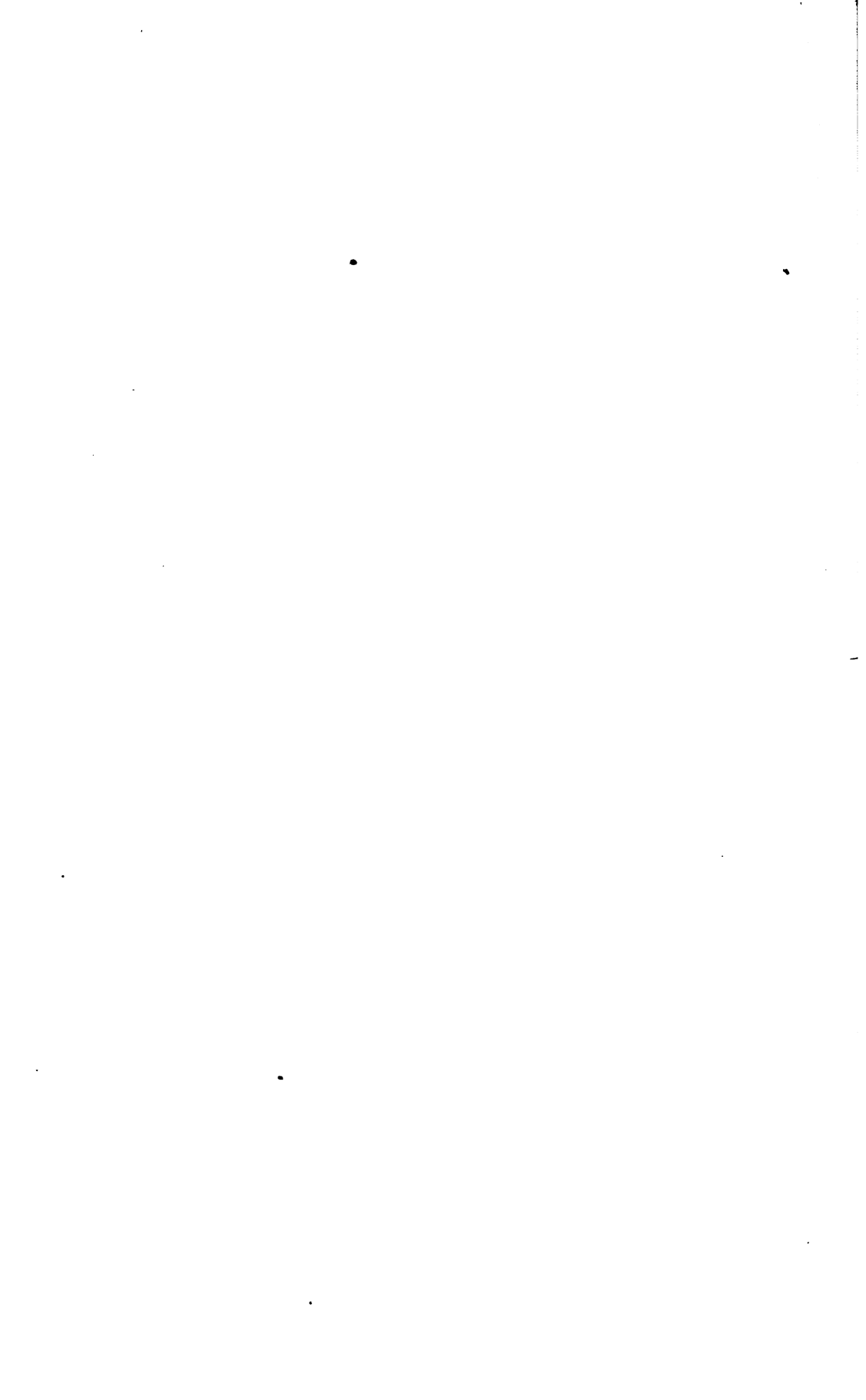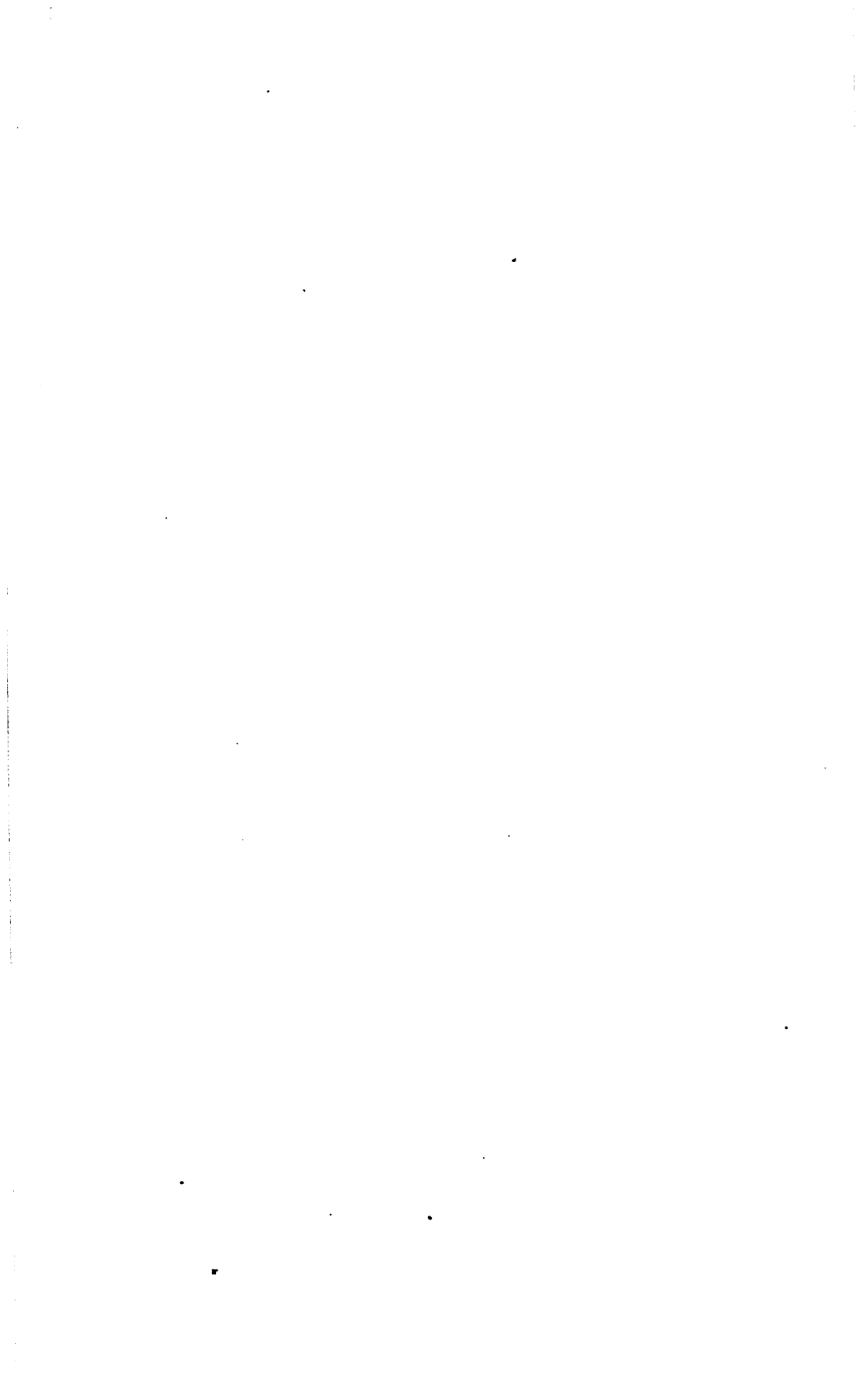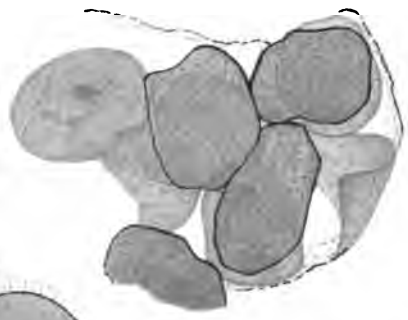
Fig. 51 a

Parasitic organisms

small chambers of inner part of disk

circumanopore chamber

Fig. 46

Fig. 52

M

2

N

Fig. 51 b

Fig. 49

Fig. 41.

Fig. 43.

brood
chambers

Fig. 42.

Protoplasm between
the young

small algae

Fig. 44.

superficial
chamberlets

Primordial
chamber

star-y grains

small algae

Fig. 46.

Fig. 48.

Fig. 47.

Nucleus.
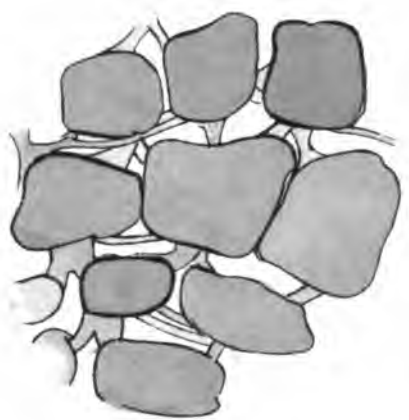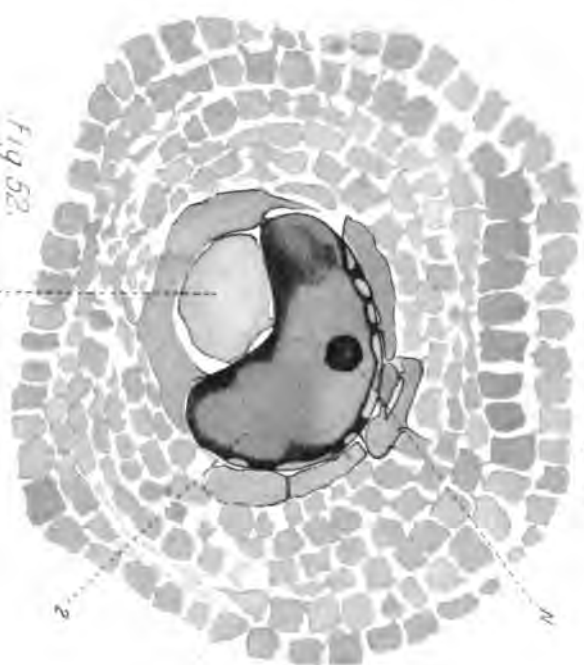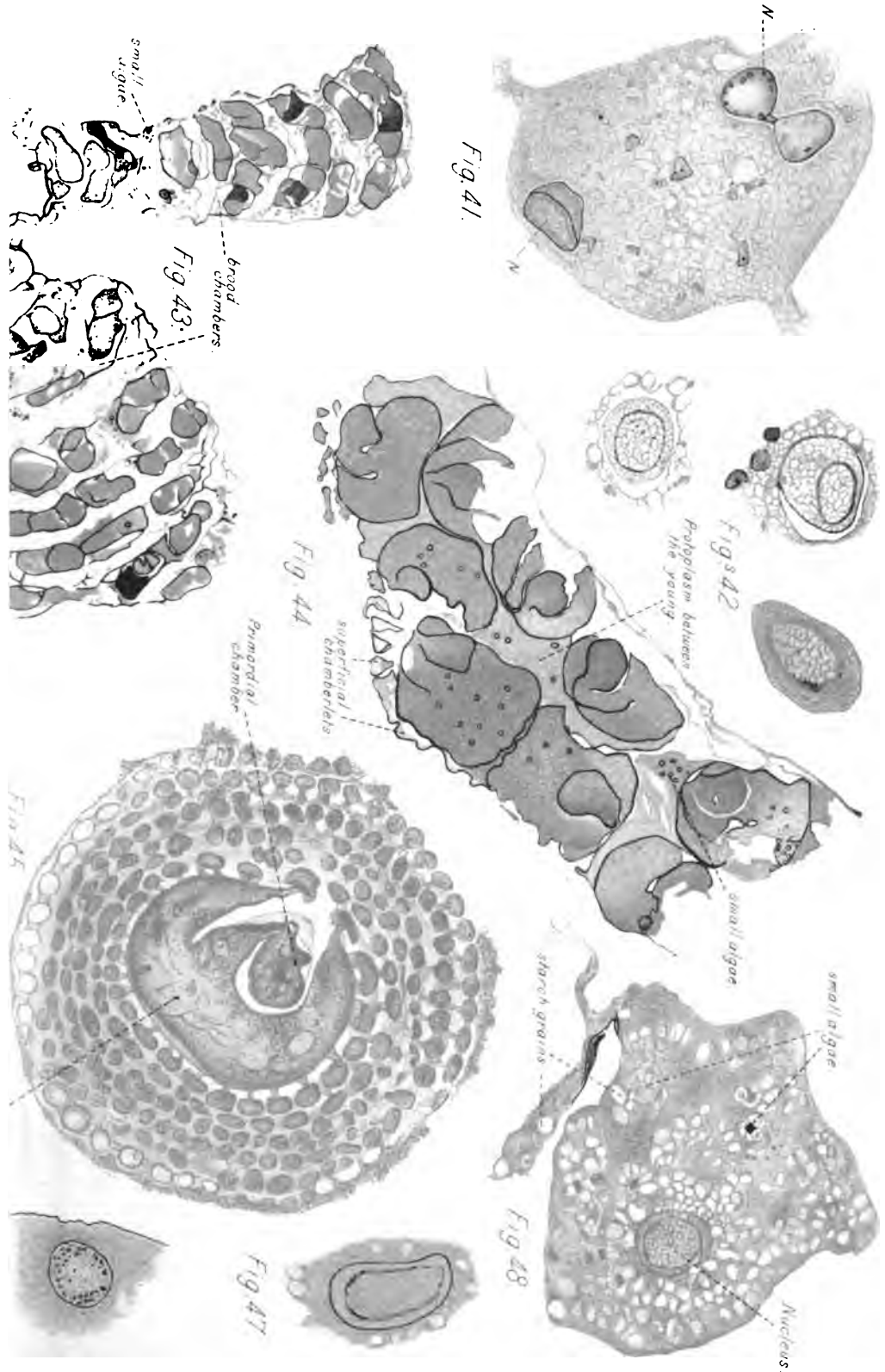
Fig. 6b.   × 690.   The inner chambers of this specimen.   The micro-sphere measures $11\,\mu \times 9\,\mu$.

Fig. 7.   × 170.   A young specimen of the microspheric form.   The microsphere measures $10\,\mu$.   f. Foreign particles collected at the mouth of the shell.

Fig. 8, a and b.   × 980.   Sections of two nuclei.   In 8a the nucleoli are vacuolated.

Fig. 9.   × 690.   A pair of nuclei, with nucleoli of different sizes.   One of the larger nucleoli is vacuolated.

Fig. 10.   × 307.   A pair of nuclei with their opposed surfaces flat, as though they had recently separated.

Fig. 11.   × 730.   Three consecutive sections through a dividing nucleus.

In (a) the two parts of the nucleus are united by a constricted band ; the right-hand part is larger than the left.

In (b) the left-hand part is larger than the right.

In (c) the left-hand part alone is seen.

Fig. 12.   × 690.   A section through three chambers, showing irregular stained strands continuous with the substance of the nuclei.

Megalospheric form.

Fig. 13.   × 170.   Specimen with thirty-nine chambers.   Megalosphere $85\,\mu \times 80\,\mu$; nucleus $98\,\mu \times 43\,\mu$.   Picro-carmine.

Fig. 14.   × 1275.   Section through the nucleus of a specimen with thirty-two chambers.   It measures $65\,\mu \times 40\,\mu$.   A large vacuolated nucleolus ($18\,\mu \times 14\,\mu$) lies in the middle.   The other nucleoli vary in size up to $4\,\mu$.   Picro-carmine, hæmatoxylin.

Fig. 15.   × 700.   Section of the nucleus of a specimen with twenty-three chambers.   It sends a process through a canal leading to another chamber.   The nucleoli are seen to be drawn out as the result of the stress to which they are subjected.   Picro-carmine, eosine, methylene-blue.

Fig. 16.   × 700.   Section of nucleus.   The reticulum is here coarser than in the nucleus shown in fig. 15.   The nucleoli vary in size up to $2\,\mu$. FLEMMING's fluid, safranin.

Figs. 17–19.   × 710.   Nuclei in optical section.   Many of the nucleoli are compound.   Picro-carmine.

In fig. 18 a large nucleolus is represented, having a vacuole in the centre, and its walls composed of bodies similar to the small simple nucleoli which lie in the reticulum.   Smaller compound masses are also present.

Fig. 20.   × 460.   Nucleus with many small vacuolated nucleoli.   Optical section.   Picro-carmine.

Fig. 21.   × 690.   Nucleus with thin-walled vacuolated nucleoli.   Their

disposition suggests that they have been set free by the breaking up of a compound nucleus. Optical section. Picro-carmine.

Fig. 22. × 1460. Part of a section of a nucleus whose nucleoli contain many vacuoles.

Fig. 23. × 250. Specimen with a "flushed" region of the protoplasm at one end of the nucleus, due to the presence of minute stained particles. Picro-carmine.

Fig. 24. × 250. Specimen showing "fragments" lying in the chambers through which the nucleus has passed, and in those immediately beyond it. In this figure the fragments have been somewhat over-emphasized, they are generally much less conspicuous.

Fig. 25. × 1460. Sections through such fragments as those shown in fig. 24. In this case they contain nucleoli. a and b are consecutive sections of the same fragment. Picro-carmine, hæmatoxylin.

Fig. 26. × 230. A nucleus which has lost its rounded form.

Fig. 27. × 250. The whole of the protoplasm, except that occupying the last two chambers, has broken up into small nucleated spheres, having a diameter of 2·5 to 3 μ. At c, a portion of the spiral canal, which lies in the umbilical region, is seen filled with similar spheres. Picro-carmine.

Fig. 28. × 1275. Part of a section of the same specimen as that in fig. 27. The nuclei which lie in the spheres are seen to be in process of karyokinetic division. Picro-carmine and hæmatoxylin.

Fig. 29. × 487. Section of nucleus with few and irregularly outlined nucleoli. FLEMMING'S fluid. Safranin.

Fig. 30. × 730. Section of the terminal chamber of a specimen of the megalospheric form, in which the large nucleus has disappeared, and numbers of small nuclei 1 to 1·5 μ in diameter are distributed in groups through the protoplasm. Picro-carmine and hæmatoxylin.

Fig. 31. Part of a section through a specimen of the megalospheric form, in which the large nucleus has disappeared and numbers of small vacuolated nuclei are distributed through the protoplasm. The structure of the protoplasm is not represented. ZEISS $\frac{1}{12}$ oil.

Fig. 32a. × 460. Section of a specimen of the megalospheric form in which the whole protoplasm is broken up into zoospores, having a diameter of 3 to 4 μ. A broad communication is seen to connect chambers 2 and 10.

Fig. 32b. × 1460. Groups of zoospores in the terminal chambers; indications of flagella are seen. In the left-hand group of zoospores the nuclei have not taken the stain.

Fig. 33a and b. × 1200. Actively moving bodies which emerged from a specimen of Polystomella crispa. Probably they belonged to another organism.

Calcarina hispida, BRADY.

Fig. 34. ×250. The inner chambers of a specimen of the megalospheric form with seventeen chambers. The nucleus is seen in the fourth chamber, sending a process into the fifth.

Fig. 35. ×250. Inner part of a specimen of the microspheric form with thirty-nine chambers. The microsphere is $13\mu \times 11\mu$ in diameter. The specimen is ill-preserved, but indications of five nuclei can be detected in some of the chambers which follow those here represented.

Fig. 36. ×56. Another specimen of the microspheric form. The inner chambers are not represented. The microsphere measured about $15\mu \times 12\cdot5\mu$. The later chambers contain numbers of young, presumably megalospheric, forms.

Fig. 37. ×250. Part of one of the chambers of the specimen shown in fig. 36, with its contents.

Rotalina Beccarii, LINN.

Fig. 38. ×170. Microspheric form. Thirty-three chambers are present. The microsphere is 13μ in diameter. Many nuclei are contained in the inner chambers.

Fig. 39. ×170. Megalospheric form. Twenty-four chambers are present. The megalosphere measures $45\mu \times 40\mu$. A single large nucleus is contained in the eighth chamber.

Fig. 40. ×460. The nucleus of another megalospheric specimen.

Orbitolites complanata, LAMK.

Microspheric form.

Fig. 41. ×760. Section through the contents of a "chamberlet." The rounded nuclei are seen to be disposed in pairs. A nucleus is in process of division, the two halves being connected by a constricted band. Alcohol, picro-carmine.

Fig. 42. ×760. Three of the larger nuclei of this form. The nuclear reticulum is distinctly seen. Alcohol, picro-carmine.

Fig. 43. ×38. Vertical radial section through the margin of the disc of a fully-grown specimen. As is usually the case in the microspheric form of the variety *laciniata*, the margin is double, hence the section is Y-shaped. The more central part of the disc is represented only by the organic basis of the walls of the chamberlets. In the peripheral portions the large *brood-chambers* are seen crowded with young. Alcohol, hæmatoxylin.

Fig. 44. ×56. Vertical tangential section through the margin of a disc whose brood-chambers contain young. Alcohol, hæmatoxylin.

Megalospheric form.

Fig. 45. × 120. Young specimen, decalcified. The centre is occupied by the "primitive disc," consisting of the "primordial chamber" (megalosphere) and the "circumambient chamber." Some six rings of chamberlets have been formed.

Fig. 46. × 540. Section of the nucleus of a very young specimen recently liberated from the brood-chambers of the parent. Hæmatoxylin.

Fig. 47. × 760. Section of nucleus of a specimen with about twenty-six rings of chamberlets. Hæmatoxylin.

Fig. 48. × 760. Section of the primordial chamber of a specimen with about thirty rings of chamberlets, showing the nucleus. Small algæ and starch grains are contained in the protoplasm. Hæmatoxylin.

Fig. 49. × 415. Section of the primordial chamber of a specimen in which the nucleus appears to have broken up into irregular fragments. About twenty-five rings of chamberlets had been formed. Picro-carmine.

Fig. 50. × 6. Part of the disc of a specimen bearing young in its brood-chambers. Decalcified. P.d. (primitive disc.) The protoplasm has left the part of the disc internal to the brood-chambers.

Fig. 51a. × 38. The young contained in the brood-chambers of the same specimen.

Fig. 51b. × 38. One of the young removed from the brood-chambers. The spaces from which the shell has been dissolved are seen dividing the protoplasm.

Fig. 51c. × 38. The empty primitive disc of the parent shell. The walls have shrunk owing to the action of the reagents.

Cycloclypeus Carpenteri, BRADY.

Fig. 52. × 56. The chambers occupying the centre of a specimen measuring about 1 centim. in diameter : M. the megalosphere ; (2) the large second chamber containing, in this instance, the nucleus. The nucleus measures 85 μ in diameter.

Fig. 53. Some of the chambers of a decalcified specimen, showing the somewhat irregular arrangement of the connecting canals.

Fig. 54. × 460. Section of the nucleus of another specimen. In this case the nucleus was in the megalosphere. It measures 60 μ × 40 μ.

On some points in the Anatomy of Nautilus pompilius.

By

J. Graham Kerr, Christ's College, Cambridge.

(PLATES IX. AND X.)

I. Introduction.

DURING the year 1893 Mr Adam Sedgwick very generously placed at my disposal a number of specimens of *Nautilus pompilius* with the suggestion that I should make an examination of their structure. The specimens were twenty-five in number, of which, however, the great majority were very young and immature. Owing to the method of preservation and to several months' sojourn in sawdust moistened with spirit, the condition of the specimens was usually such as to render them unfit for histological study. Fortunately one of them was sufficiently good to allow the use of the section-method to confirm the results of minute dissection. In the following somewhat fragmentary paper it is my purpose to touch upon what seem to me the more important points at which I have arrived, hoping at some future date, if able to obtain properly

preserved specimens, to extend my investigations and to fill up the obvious lacunæ.

I can hardly adequately express the obligation under which I am to Mr Sedgwick for the generous gift by which he has made these investigations possible and opened the way to what, however poor its results are so far, has proved a study of absorbing interest, and also for much kind advice and encouragement. To Mr Wilson also a word of thanks is due for the care with which he has attended to the illustrations.

II. The Body-cavity of Nautilus.

It is now generally recognized that the body-cavity in the *higher* Metazoa may be referred to either of two very distinct types. The first of these, typically developed in Annelida and Vertebrata, is lined by a definite characteristic epithelium, from some of whose cells arise the genital products, while others become the renal excretory cells. It appears at an early stage in development as a more or less continuous space, and it communicates with the exterior by apertures in the body-wall. To a body-cavity of this type it is advisable to restrict the term *Cœlom*.

The second type of body-cavity is to be found in the Mollusca and Arthropoda generally. It is part of the vascular system, through it is pumped a continuous stream of blood by the heart, and it does not communicate with the exterior. It may be looked on as being formed by the expansion of the terminal parts of the blood-vessels into large sinuses whose walls have, to a greater or less extent, disappeared, giving rise to a sponge-work more or less sparse according to the extent to which this process has gone on. This type of body-cavity was named by Sedgwick, *Pseudocœl*; by Lankester, *Hæmocœl*. The word cœlom has been used with such looseness that Lankester's term is perhaps to be preferred; all the more so as it specifies in itself one of the main characteristics of this form of body-cavity.

Occurring well-developed in Annelids, at least allied in all

probability to the ancestral forms of Molluscs and Arthropods, the coelom is to be looked on as the more primitive of the two types of body-cavity above-mentioned; and it looks as though within each of the two latter groups it had gradually dwindled and become supplanted and replaced as the functional perivisceral cavity by the ever increasing hæmocœl.

In most Cephalopods the cœlom still takes a large part in the formation of the perivisceral cavity, and in *Nautilus*, corresponding with its more archaic character, this is so to a greater extent than in any of the other Cephalopods.

The hæmocœl of *Nautilus* is specially developed in the headward section of the body. A sagittal incision through the body-wall just behind the hood exposes to view a large chamber in which lies the pharynx as well as the vena cava, several large nerve-trunks, and a single loop of the intestine. This cavity is the main division of the hæmocœl; ventrally it is bounded by the body-wall and the muscular substance of the hood, etc., into which it extends in numerous sinuses, while dorsally and towards the apex of the visceral hump it is bounded by a thin and delicate but complete membranous septum which forms the boundary between it and the cœlom. The inner ("ventral") face of this septum has a rough and spongy appearance, and little connective-tissue strands pass from it to the surface of the pharynx. These delicate threads of connective tissue traversing the cavity and slinging up its contained organs at once suggest the hæmocœlic nature of this part of the body-cavity: and the conjecture is confirmed on raising up the pharynx, for one then sees that the upper wall of the vena cava is perforated by numerous foramina, some of considerable size, which put its cavity into free communication with that part of the body-cavity now under discussion. These foramina were described and figured long ago by Owen, in his Monograph, but they appear to have been unnoticed by subsequent observers[1].

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[1] Since writing the above I see that Pelseneer in his recent *Étude des Mollusques*, p. 191, says that "la cavité viscérale est un vaste sinus communiquant avec la veine cave par des orifices percés dans la paroi de celle-ci."

The true cœlom (*viscero-pericardial sac*, Owen) has received comparatively little attention from previous investigators,

FIG. 1.
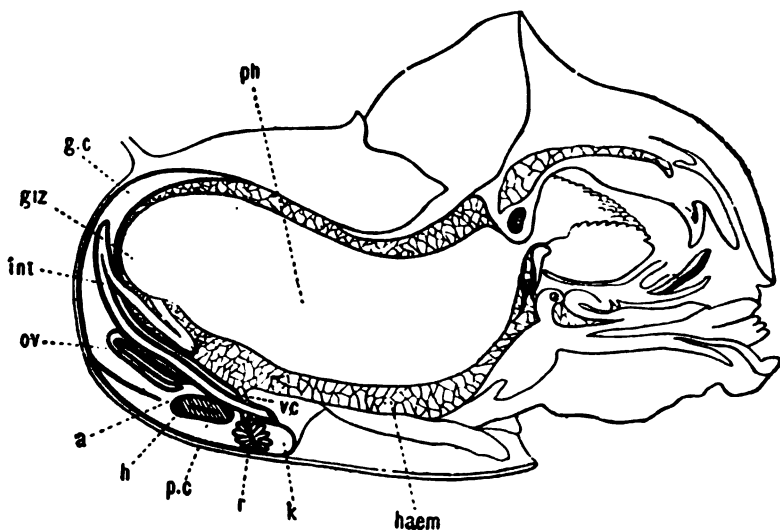
Sagittal section through *Nautilus*.

Diagrammatic sagittal section through the animal of a young female of *Nautilus pompilius*, to show the general relations of the cœlom and hæmocœl. (The section really passes very slightly to the right of the mesial plane, so as to traverse one of the renal chambers.)

haem, hæmocœl; g.c, genital division of the cœlom; p.c, pericardial division of the cœlom; a, aperture in septum dividing g.c from p.c; k, right inner kidney-chamber; r, pericardial gland corresponding to this kidney-sac; h, ventricle; ov, ovary; ph, crop; giz, position of its opening into the gizzard, which lies to the left of the plane of section; int, intestine; v.c, vena cava.

Grobben and Lankester being the only authors who devote to it more than a few passing words[1].

It is convenient to treat together the cœlom itself, the

[1] Pelseneer, *op. cit.* p. 192, says that the cœlom "s'étend dorsalement, autour de l'estomac, jusque vers la moitié de l'œsophage. Il contient, outre le cœur, la glande génitale, la veine cave et une partie des appendices glandulaires des vaisseaux branchiaux afférents,"—a statement which is obviously at variance with the account here given in two important respects.

excretory and the genital organs as forming all parts of the same organic complex. On reference to the diagrammatic longitudinal section through the animal, it is seen that the cœlom is limited to the aboral end of the body, where it forms a flattened space immediately underlying the body-wall— between this latter and the thin membranous bag which limits the cavity of the hæmocœl. The cœlomic cavity is divided by an oblique septum into a large upper division (*g.c.*), the genital division of the cœlom, and a smaller lower pericardium (*p.c.*). The septum separating these is not quite complete, being perforated by three apertures of considerable size. One of these is indicated in the diagram at *a*.

The Genital division of the Cœlom (*g.c.*) is, as already mentioned, the larger of the two cœlomic chambers. It occupies the extreme aboral (dorsal) end of the body, and is lined throughout by a delicate epithelium composed of flattened plate-like cells usually hexagonal in outline, the cell-boundaries, however, being very indistinct. Each cell contains a rounded nucleus with chromatin network and one or two small nucleoli. Into this division of the cœlom project the gizzard, the greater part of the length of the intestine, and the genital gland. It must of course be remembered that all these organs are invested by the cœlomic epithelium, so that it is only in a certain sense that they can be said to be situated *within* the cavity. The genital gland being merely a specialised part of the wall of the cœlom, it may appropriately be shortly described at this point.

The Ovary is a flattened ellipsoidal body attached by a mesovarium to the lower (posterior) side of the intestine, and at its oral (ventral) end having a considerable aperture which throws its cavity into continuity with that of the surrounding cœlom. The general characters of the ovary are shown in fig. 2, representing a sagittal section through the organ of an immature female. The ovary exists here in almost its simplest possible condition, in the form of a specialized ovigerous area of the cœlomic epithelium roofed over and protected by a simple upgrowth from the cœlomic wall. The outer surface of the

organ is covered over by the general epithelium of the cœlom, having the characters already mentioned, and at the opening at the oral (ventral) end of the ovary this is inflected into its interior so as to line this likewise. The cavity of the ovary is

FIG. 2.
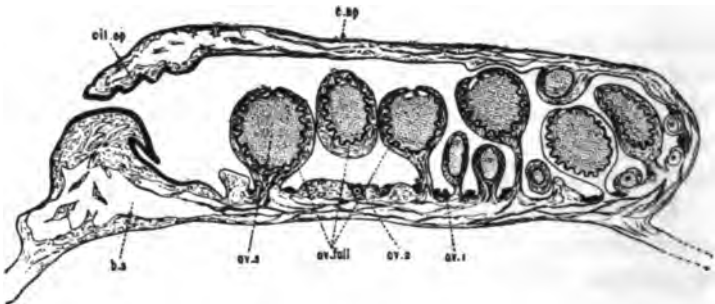
Longitudinal section through ovary of a young *Nautilus*.

c.ep, cœlomic epithelium covering outer surface of the ovary; *cil.ep*, ditto reflected into aperture of ovary; *ov.foll*, ovarian follicles; *ov.* 1, 2, 3, ova in various stages of development; *b.s*, blood-sinuses in the wall of the organ.

thus merely an incompletely shut-off portion of the cœlom. Traced into the interior of the ovary, the epithelium about its opening assumes a columnar form and bears long cilia (*cil. ep.*). Along its roof the cells become shorter and eventually cubical. About two-thirds of the way from the mouth of the cavity the ovigerous region is reached, and this occupies the remainder of the roof and nearly the whole of the floor of the ovary. The ovigerous region of the cavity is thickly beset with egg-follicles of various ages (*ov. foll.*). In the recesses between the bases of these the lining epithelium—a thin protoplasmic layer with scattered nuclei and indistinct division into cells—thickens up into syncytial masses of protoplasm containing large round nuclei, each with a large deeply staining nucleolus, around which the protoplasm tends to segregate off more or less distinctly. The primitive ovum develops within such a heap, the nucleus increasing in size and assuming more and more the

character of a "germinal vesicle," and the protoplasm first becoming more distinctly aggregated round the nucleus and marked off from the surrounding protoplasm and then increasing rapidly in size. As the ovum increases in size the substance of the ovarian wall grows up round it to form the follicle, while the syncytium accompanying the ovum apparently gives rise to the lining-cells of the follicle. The latter are pear-shaped structures borne on stalks, which are usually simple, but occasionally branch, thus showing a tendency towards the condition in *Argonauta*, where they are much branched and tree-like. Externally the follicle is covered by a very thin epithelium, which distally becomes continuous with the lining layer of "follicle cells"—a layer of thick columnar cells immediately surrounding the egg. In the young follicle this layer runs concentrically with the outer surface of the epithelium, but as the egg increases in bulk an increase in the surface of this apparently nutritive organ becomes necessary and the follicle-epithelium grows inwards as a series of anastomosing folds. On this account the older eggs when removed from the follicle show on their surface a network of deep fissures formed by the follicular epithelial ingrowths. In the oldest female specimen accessible, unfortunately too macerated to make out many details, the eggs had reached a large size, over 10 mm. in length, and their substance was already enormously yolk-laden, the protoplasm being practically restricted to a small cap on the end of the egg next the follicular opening. Imbedded in this was the large nucleus with densely staining nucleolus. The presence of a definite opening in at least the older follicles and the position of the egg-nucleus close to this, suggest the possibility of fertilization in *Nautilus* being internal; and the great size of the eggs and their yolk-laden character point to the segmentation being meroblastic as in other Cephalopoda.

The wall of the ovary, as of other important organs, is loose and spongy, traversed by extensive blood-sinuses (*b.s.*). Prolongations of these pass up the stalks of the follicles, and form a specially developed layer immediately underlying the follicle-epithelium—a condition to be correlated with the provision of

an abundant blood-supply to satisfy the needs of the glandular epithelium.

The Testis is, in its main morphological features, quite similar to the ovary; in other words, it is an invaginated area of the lining of the cœlom. Only in the testis great increase in the area of the germinal epithelium has been brought about by the involuted portion of cœlomic epithelium, instead of remaining a simple sac, becoming divided up into a system of delicate branched tubes.

In an apparently adult specimen, the testis was a large brownish organ of roughly triangular shape, its rounded apex directed upwards and towards the right side. Its apical portion was in close contact with the body-wall, while its basal part was separated from the body-wall by the pericardium.

The testis is slung up by a strong ligamentous band about 1 cm. broad to the tunic of the gizzard, by a similar but broader band which is attached along a sagittal line to the body-wall (the root of the siphuncle being about the middle of its line of attachment), and finally along its anterior face by a thin peritoneal fold to the loop of the intestine. Further, at its lower end the epithelium covering the outer surface of the testis is continued into that covering the pericardial septum and heart. Near the inferior angle of the organ is its aperture— a slit about 2 mm. in length, bounded by two flat, much projecting lips, which, lying closely opposed to one another, project into a deep recess covered by a crescentic flap, the internal opening of the vas deferens. Thus, though the cavities of the testis and of the vas deferens open quite independently into the cœlom, they are at least during sexual maturity *functionally* continuous with one another.

In a section through the testis of a young individual, the aperture of the organ is seen to lead into a vestibule into which open several straight ducts. Each of these, traced inwards, divides up into numerous tubules which end blindly and are aggregated into distinct lobes and lobules. Vestibule and tubes are lined by epithelium continuous with that of the general cœlom. The wall of the organ is traversed by a sponge-work of

blood-sinuses. Between the lobules these are greatly developed, their separation walls being reduced to fine connective tissue-threads serving to bind the lobes together. Into the substance of the lobules also pass continuations of the sinuses. Regarding the character of the epithelium in different parts of the tubes, the state of the specimens does not allow me to say anything.

The Pericardium or inferior chamber of the cœlom is considerably smaller than that already described. It immediately underlies the " postero-dorsal " body-wall throughout its half next the mantle-flap, and its cavity is conveniently exposed by reflection of its external wall. It is then seen to be quadrangular in outline, rather broader than long (68 mm. × 54 mm. in one specimen). From its inner (anterior) wall, in a curved row parallel to the ventral (oral) border of the chamber, project the four clusters of pericardial gland-follicles. The external pair are in such a view (*i.e.*, from posterior) partially hidden by a broad frænum, which on each side connects the anterior wall of the chamber with the posterior wall. Dorsal (aboral) to the two central pericardial glands is seen the ventricle firmly bound down to the anterior wall of the chamber—the epithelium lining which is reflected over its surface. Just dorsal to the ventricle a large rounded aperture leads into the genital division of the cœlom, and ventral to it is a still larger such opening. The four auricles attached to the corners of the ventricle, unlike it, hang quite free in the pericardium. In some specimens these were markedly asymmetrical, those of the left side being much more dilated than those of the right.

Each of the divisions of the cœlom above described is in open communication with the exterior. In the case of the pericardium, one finds at its ventral end that the cavity is prolonged on either side on the anterior face of the frænum mentioned. Each such prolongation forms a small somewhat triangular chamber with its greatest diameter transverse, and this at its mesiad end opens into the mantle-cavity by the tumid lipped, so-called viscero-pericardial aperture. The genital division of the cœlom primitively possesses at its ventral end also a communication upon each side with the exterior. In the

actual animal, however, one of these has become closed intern-
ally, as Lankester has shown, while the other persists in the
female as the oviduct, in the male probably as the part of the
functional genital duct extending from its cœlomic opening to
the inner end of Needham's sac.

On pulling the mantle dorsalwards, so as to afford a view of
the interior of the mantle-cavity, such as that shown in
Lankester and Bourne's figure, one notices a little distance to
the headward side of the root of each gill one of the four
kidney-openings. These are arranged in two pairs. Just to
the mesiad side of each of the posterior openings, one sees the
slit-like viscero-pericardial apertures, leading, as above men-
tioned, into the pericardium.

This condition in *Nautilus*, where the viscero-pericardial sac
opens independently of the kidney, is homologized, and no doubt
rightly so, with the condition met with in *Spirula* and *Ægopsids*,
where the viscero-pericardial canal opens into the kidney-sac
near its mouth, by supposing the opening of the latter to have
migrated on to the outer surface (Grobben, Lankester), an
identical process to that which has taken place in, *e.g.*, the
genito-urinary passage and the rectum in Mammals.

Accompanying the anterior kidney openings no such
pericardio-visceral pores are seen, and in consequence of this it
has been concluded that the anterior and posterior kidney-sacs
are not serially homologous. All agree in regarding the posterior
one as primitive, but the anterior sac is looked on as a secondary
formation—either as a secondarily arising repetition of the
posterior one, or as having been split off from it in correlation
with the development of a new gill and new afferent vessel
(Grobben).

As a matter of fact, however, such a viscero-pericardial
aperture *is* present, corresponding to the anterior kidney-open-
ing. It is the primitive genital aperture. Such is seen either
in the case of the oviduct or of the rudimentary left genital
duct of either sex[1]. This opening leads into the genital division

[1] In the case of the functional genital duct of the male, a shifting of the
external aperture has taken place through the, in all probability, *secondary*
development from the adjoining body-wall of the penis.

of the cœlom just as does the viscero-pericardial pore into the pericardium, and, like it, is situated mesiad to the kidney-opening. The only striking difference is, that this pore is normally rather farther apart from its corresponding kidney-opening than is the viscero-pericardial pore. The latter is normally quite close to its kidney-opening, but its distance from it is very variable and may reach 3 mm.

It appears to me that there can be no question as to the homology of the two sets of apertures. In the genital segment, however, the migration of the cœlomic aperture has gone a little further beyond the bounds of the kidney-sac. Each cœlomic duct, plus its kidney-sac, would on this view correspond to an ordinary "nephridium," *i.e.*, a tube leading from the cœlom to the exterior, part of the wall of which has taken on an excretory function. In the Dibranchs, in correlation with the disappearance of the anterior gill, the corresponding kidney-sac has disappeared, while its cœlomic duct persists as the genital duct. The genital ducts of the Cephalopoda in general then are nephridia[1], minus their excretory sacs.

III. THE MALE GENITAL DUCTS AND PENIS.

The general disposition of the genital apparatus in the male is shown in fig. 3 (p. 192). As is well known, only the duct of the right side is functional in *Nautilus*. On the left side there is the "pyriform sac" of Owen, shown by Lankester and Bourne to represent the left genital duct, although the question was left open by them—whether it represented *only* the genital duct, or the genital duct together with the genital gland of the same side[2].

From the large cœlomic aperture the genital duct passes through the quadrangular "accessory gland" composed of

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[1] Pelseneer asserts that the genital ducts of Cephalopods are nephridia—without, however, qualifying his statement or supporting it by evidence.

[2] That it represents only the duct appears to me to be shown by the condition in the very young animal, in which the inner part of the genital duct has exactly the appearance of the pyriform sac in the adult—the rudiment of the gonad being quite distinct and apparently median and unpaired.

numerous cæcal tubular outgrowths from the duct itself.
Beyond this point the duct opens into the spermatophore sac—
a large structure somewhat elliptical in outline when seen from
the anterior (dorsal) or posterior (ventral) aspect (Pl. X. fig. 1).
The vas deferens opens into this at its outer end. Internal to
this opening there begins a longitudinal septum which divides
the cavity of the sac through about half its length—terminating

FIG. 8.
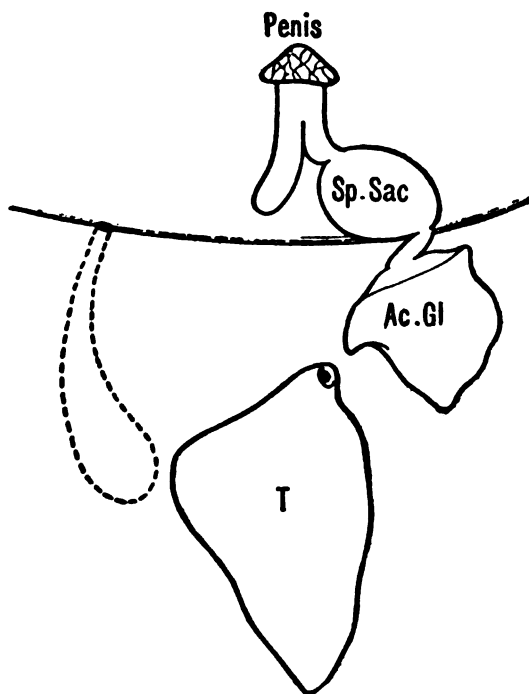
Diagram of the testis, genital duct, and penis of the male *Nautilus.* The rudi-
mentary genital duct of the left side is dotted in.

T, testis: at its upper end is seen its aperture into the general cavity of the
cœlom. Ac.Gl, accessory gland with internal opening of the vas
deferens beneath the crescentic flap at its left-hand corner. Sp.Sac, sper-
matophore sac.

The curved line traversing the diagram from side to side represents the line
along which the mantle-flap is reflected headwards.

in a free concave edge. In the sexually mature animal the much coiled-up spermatophore mass occupies the cavity of the sac bending round the edge of the septum. The internal surface of the sac-wall is smooth to the naked eye, while a low-power lens discloses the existence of minute glandular-looking rugæ running on the whole parallel to the axis of the spermatophore mass.

At its anterior inner corner the cavity of Needham's sac passes into the penis. This is a somewhat cylindroidal, flattened structure about 10 mm. in length and 8 mm. greatest breadth, attached to the body-wall within the mantle-cavity. Its walls are thick and muscular, and its cavity is divided by a sagittal longitudinal septum, which does not extend quite to the tip of the organ, into two moieties. Of these it is only the right with which the sac of Needham communicates, the left being (as will appear later) connected merely with a peculiar blind sac. The right penial cavity is somewhat semi-pyriform, becoming narrower distally. Its lining is thrown into large, smooth, glandular-looking rugæ, which anastomosing with one another form a kind of raised network with elongated meshes. Outside this lining is the muscular coat about 1·5 mm. thick and largely composed of radial fibres. The muscular layer is traversed by an extensive system of blood-spaces. This is most developed towards the "posterior" end of the penis. It forms a distinct layer near the outer surface of the organ, but its spaces also, though less conspicuously, ramify hither and thither in the general substance of the muscle.

The left penial cavity is cylindroidal in form, and its diameter only about half that of the right cavity at its widest part. The inner surface of its wall is also thrown into folds; but these are mainly longitudinal, parallel, and do not anastomose to the same extent as do those of the right cavity. The lining-tissue is of a less deep colour and less glandular-looking; the muscular wall is thinner, and the cavernous layer is also less developed.

At its "posterior" end, about the level of the point at which the right cavity becomes continuous with the sac of Needham,

the left cavity diverges towards the left side, much as the long axis of the Needham's sac does towards the right, and gradually expands into a flask-shaped sac, in this specimen 6 mm. long by 3 mm. broad. This is rounded off and ends blindly. The inner surface of its wall exhibits faint longitudinal corrugations. It is difficult to believe that this left moiety of the penial apparatus does not represent the reduced fellow of the right moiety, i.e., of the right penial cavity plus the sac of Needham. On the left side, however, the rudimentary vas deferens does not communicate with the penial sac, but opens, as is well known, directly into the mantle-cavity. The position of this external aperture corresponds very closely to that of the opening of the vas deferens into the spermatophore sac on the opposite side. The whole arrangement strongly suggests that of the functional male genital duct, only that portion from the cœlomic aperture to its opening into the sac of Needham represents the primitive duct, and that the Needham's sac and the penis are secondarily added structures developed from the adjacent wall of the mantle-cavity. In the young animal, the Needham's sac being not yet expanded, the form and size of the right portion of the apparatus are in almost exactly the same condition as is the left in the adult.

IV.   The Buccal Nervous System.

Lankester[1] says, in speaking of *Nautilus*:—"No buccal nervous system has been observed in *Nautilus*;" and again, "nor has an enteric nervous system been described in this animal." In regard to both these statements, Professor Lankester seems to be in error, as a complicated buccal system was described and figured by H. v. Jhering[2], while at least part of an enteric system was described by Keferstein[3]. In regard to the buccal nervous system it seems advisable to give a short

[1] *Zoological Articles*, p. 142.
[2] *Vergl. Anat. des Nervensystems der Mollusken*, p. 263.
[3] Bronn's *Thierreich*, Malacozoa, p. 1373.

account, however, as von Jhering's remarks are very brief, while in the construction of his diagram a curious blunder seems to have been made, which has been perpetuated by its being copied by leading text-books. In effect, what he figures as the cerebro-pharyngeal connective is really the forward prolongation of the pharyngeal ganglion, which, uniting with its fellow in the middle line, forms the anterior infra-buccal commissure. On the other hand, the two nerves figured as emerging from the pharyngeal ganglia laterally are the cerebro-pharyngeal connectives, of which there are not one, but two, on each side. In fact, by rotating the portion of his figure representing the buccal nervous apparatus through 180° about an axis passing through the pharyngeal ganglia and joining up at the cut ends as indicated above, one gets quite an accurate diagram. No doubt v. Jhering's slip arose through dissecting and figuring this part of the nervous system after the buccal mass had been removed from its connection with the animal.

The cerebro-pharyngeal connectives are two thick nerve-trunks on each side, taking their origin from the adoral border of the supra-œsophageal nervous mass. Enclosed in a dense sheath of connective tissue, they pass to the sides of the buccal mass. For the first part of their extent their course is highly sinuous, a character probably to be connected with the protrusibility of the buccal mass and the consequent very variable distance between it and the fixed circum-œsophageal parts of the nervous system. Pursuing a slightly convergent course the two connectives reach the lateral aspect of the buccal mass, and there unite in the pharyngeal ganglion (fig. 4, *ph. g.*)—a triangular structure with its apex directed towards the mouth—and another of its angles external. It lies on the muscles of the buccal mass immediately beneath the skin.

The two pharyngeal ganglia are connected to one another by a longer anterior and a shorter posterior commissure, on the course of the latter being the slightly swollen " buccal ganglia." The anterior commissure (fig. 4, *ant. com.*), figured by v. Jhering as cerebro-pharyngeal connective, is a flattened band nearly 1 millimetre in breadth, and pursuing a ∩-shaped course

immediately beneath the skin, and just within and parallel to the margin of the lower mandible. As the ganglion tapers off into the commissure, it gives off numerous small and several larger filaments to the skin-fold surrounding the mandibles.

Fig. 4.
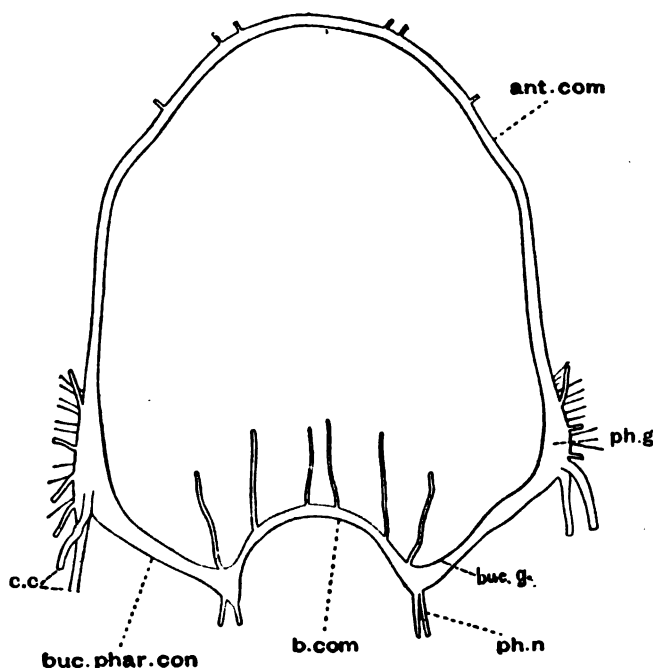
Buccal nervous system of *Nautilus pompilius.*

ph.g, pharyngeal ganglion; *buc.g.,* buccal ganglion; *c.c,* cerebro-pharyngeal connective; *buc.phar.con,* bucco-pharyngeal connective; *ph.n,* pharyngeal nerves; *b.com,* buccal commissure; *ant.com,* anterior pharyngeal commissure.

From the adoral part of the commissure also some very fine strands pass off to the same structures.

The internal angle of the pharyngeal ganglion is prolonged towards the middle line into the posterior commissure, which soon swells out slightly, forming the buccal ganglion (*buc.g.*).

From this pass backwards two nerves into the sponge-work of the pharyngeal wall (*ph.n.*). Whether they are continued back in this along the sides of the crop to become connected with the gastric ganglion, I was not able satisfactorily to determine. From the aboral end of the buccal ganglion anteriorly a twig passes to a large elevation of the buccal lining, within which it divides up into numerous branches. At its oral end the ganglion passes into the short convex-forwards commissure which connects it with its fellow. From this two nerves pass adorally on each side, the smaller more mesially situated immediately underlying the radula.

V. The Innervation of the "Inner Inferior Lobe."

Posterior (ventral) to the buccal mass, well within the hood-tentacle complex, is a flattened lobe, bearing on each side a series of tentacles, separated by a peculiar lamellated organ which has been supposed to be sensory. This lobe is called the "inner inferior lobe" by Lankester. For its innervation there is figured by Owen, and copied by Gegenbaur and others, a small distinct ganglion on each side. In the specimens which I have dissected, however, the conditions are as follows :—Upon each side, somewhat external to the root of the funnel-nerve, there arises from the anterior sub-œsophageal nerve-cord a rather thinner nerve-trunk, which passes into the basal part of the lobe mentioned. This bends towards the middle line, pursues a curved course in the substance of the lobe, and meets with its fellow of the opposite side. The two together form in fact not two separate ganglia, but a continuous cord. The median most strongly curved part of this cord gives off about 24 slender nerve-filaments, which radiate forwards to the lamellæ of the lamellated organ. The more lateral parts of the cord, on the other hand, give off a stout unbranched nerve to each of the tentacles of the lobe. These nerves, coursing as they do through the fibro-muscular substance of the lobe, are very hard to trace out in their entirety.

VI. THE POST-ANAL PAPILLÆ AND NERVES.

A short distance behind the anus is a peculiar flap-like structure, arising from the body-wall and bearing four papillæ. It varies much in form—sometimes being divided into two distinct halves—sometimes continuous mesially—sometimes thin and membranous—sometimes tumid and swollen. It is covered by columnar epithelium, and filled with ordinary connective tissue, sometimes with abundant jelly-like matrix.

FIG. 5.
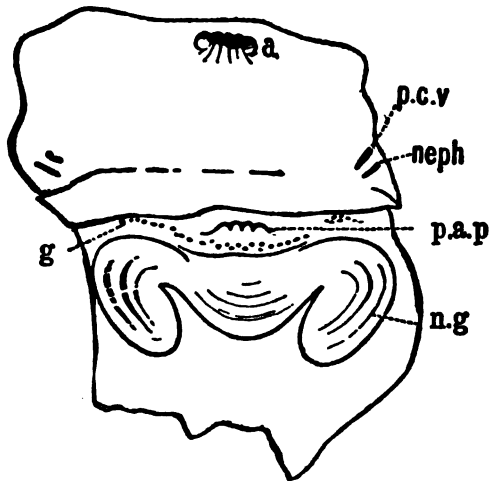
Post-anal papilla with glands in the female.

a, anus; p.a.p, post-anal papilla; g, openings of glands; n.g, nidamental gland; p.c.v, pericardio-visceral aperture; neph, opening of kidney chamber.

In the female, examination of this region with a hand-lens shows the existence of a large number of apertures in the outer skin. These, to the number of about 150, form a band about 0·5 mm. in width, curving gently forwards on either side of the post-anal papilla, tapering off and terminating close to the advehent vessel of the posterior gill. In section these openings are seen to be the apertures of tubular ducts which pass inwards perpendicular to the surface for some little distance

and then break up into several blindly ending branches. These are lined by involutions of the surface epithelium, which in the neighbourhood of each aperture increases to about twice its thickness elsewhere, its celia at the same time becoming extremely long and powerful (·03 mm. in length). Once within the narrow aperture the lumen of the tube expands to about ·05 mm. in diameter, and the lining epithelium becomes shorter, the remainder of the lumen being lined by comparatively short columnar cells, each with a round ellipsoidal nucleus.

Arising from the posterior side of the posterior sub-œsophageal nerve-cord, close to the middle line, are a pair of stout nerve-trunks, which pass backwards on either side of the vena cava. The greater part of these pass off to supply the gills, but a direct prolongation of each is present, which passes backwards on either side of the post-anal papilla. This nerve is largest in the female, where it gives off nerves towards the middle line, supplying the nidamental gland. In the region of the post-anal papilla branches also pass off towards the middle line. There appears to be—although the condition of the material did not allow me to quite satisfy myself on this point—an anastomosis of these centrally passing branches with those of the opposite side. If this be confirmed we have here a true post-anal commissure, such as exists in *Chiton*: in which case we should be compelled to regard not merely the "posterior sub-œsophageal nerve-mass," but rather the two lateral portions of this, together with the nerve-trunks which have been mentioned as passing backwards on either side of the vena cava, as forming the homologue of the pleuro-visceral nerve-cord of *Chiton*. The mesial part of the posterior sub-œsophageal nerve-mass would then represent a secondary fusion between the nerve-masses of the two opposite sides.

VII. THE SPERMATOPHORE-RECEIVING APPARATUS.

Behind (ventral to) the buccal mass and immediately underlying the inner inferior lobe, the kind of shelf which connects the tentacular mass of one side with that of the other has its inner surface raised into a series of curious lamellæ.

The remarkable organ formed has been referred to by Valenciennes[1], and by Lankester[2], as a paired structure. Not always, however, does it seem to be so, as in one of the two specimens in which I observed it the laminæ were quite continuous across the middle line, the laminæ appearing in fact to be mere exaggerations of the fine transverse wrinkles into which the surface of the skin is thrown behind the lamellar organ. Of the two authors referred to, the first, after some hesitation, suggests that the lamellated organ may be tactile in function, "analogous to the palpi round the Crustacean mouth." Lankester, on the other hand, for what reasons is not stated, very definitely describes the organ as "probably olfactory[3]."

During the examination of a mature female somewhat startling evidence was obtained as to the true function of this organ. The lamellæ were here covered with a thick coagulated material apparently secreted by them, spreading over the edges of the lamellæ and passing in thin plates down between them. Partially imbedded in the coagulum on the left side and only partially visible, there appeared a peculiar brown structure which at once suggested the appearance of a spermatophore. And upon carefully clearing away the surrounding material the surmise so suggested was corroborated. The long slender spermatophore lay coiled backwards and forwards over the surface of the lamellæ in the manner indicated in Pl. X. fig. 2, held firmly in position by the coagulated material.

We would seem to have here a peculiar cement-secreting glandular apparatus, on whose sticky surface the spermatophore is deposited by the male.

In other Cephalopods the position in which the spermatophore is attached to the female varies: in Œgopsids, Octopods, and Sepiola, e.g., it is passed into the mantle-cavity; in other Decapods (e.g., Sepia, Loligo) it is attached to the skin on the outer surface of the buccal mass. In Nautilus the position is thus a somewhat intermediate one.

[1] Arch. Mus. d'Hist. Nat. tom. ii. p. 277.   [2] Zoological Articles, p. 130.
[3] Op. cit. fig. 88.

VIII. The Morphology of the "Arms" of Cephalopods.

As Grobben has justly remarked, and as Pelseneer has adopted as text to his paper on the subject "eine der schwierigsten Fragen in der morphologischen Deutung des Cephalopodenkörpers bildet die Morphologie der Kopfarme"; and in accordance with this, as well as with its far-reaching interest, the question has attracted from time to time a great amount of attention from morphologists.   Regarding the fundamental nature of these organs, two very different views have been brought forward :—

> (1)   That the arms of the Cephalopods are processes of the head or circumoral region.
>
> (2) . That they are processes of the foot, part of which has grown up on either side so as to finally surround and almost completely hide from view the head itself.

To enter in detail into the differences as to minor points in the tenets of the various upholders of these two views seems unnecessary, as this has already been done by others[1]; and further, because it is proposed to consider the problem here in its most general aspect—as to whether the Cephalopod arms are cephalic or pedal.

It may be advisable, in the first place, to inquire whether there is anything in the general relations of the parts to support or even suggest the second of these views.   In ordinary Cuttlefishes it is pretty obvious that there is nothing of the kind—the arms form a continuous circle round the buccal mass—one would naturally suppose they belong to the head.   It is therefore important to glance at *Nautilus*, where, as Lankester has well accentuated, "any divergence from the condition obtaining in other forms has possibly, and even probably, a special significance," and " is not readily to be dismissed as an 'adaptation' peculiar to that form[2]."

[1] *Cf.* especially Pelseneer's admirable summary, '*Challenger*' *Report*, Pteropoda.

[2] *Quart. Journ. Micr. Science*, vol. xxiii. p. 348.

In *Nautilus* the arrangement of the circumoral lobes and tentacles has been described by Bourne and by Lankester, so that it is unnecessary to go into details. Anteriorly (dorsally) is the large fibrous mass of tissue which forms the hood. Laterally, on each side, is an aggregation of tentacles. Anteriorly (dorsally) the mass of tentacle-sheaths is directly continuous with the hood. On slicing away the substance of the hood carefully, it is seen that the bases of all the outer tentacles are embedded in it. The appearance of tentacle-sheaths is due merely to the more or less distinct marking off by superficial grooves of the parts of the mass surrounding each tentacle. Hood and tentacle-sheaths together form a perfectly continuous mass lying anterior (dorsal) to the buccal mass and curving backwards (downwards) on either side of it in saddle-like fashion. In the male this is very obvious, the two limbs of the mass being connected together posteriorly merely by a thin shelf. In the female, however, this bears on its inner side the "inferior inner lobe," which bears on each side a group of tentacles and whose appearance suggests a bilateral origin. The main impression given by the tentacle-hood complex is that of a saddle-shaped structure, situated anterior (dorsal) to the buccal mass—its limbs passing backwards on either side of the latter. The anterior (dorsal) part of the complex here predominates : it is developed less equally all round the buccal mass than in Decapods ; its preponderating part is dorsal.

The next point of interest in the gross anatomical relations of the parts lies in the funnel which, according to the upholders of the "pedal" view, is primitively continuous with the tentacle-hood mass.

The Funnel.—This is a large tongue-shaped structure attached to the posterior face of the body—to the roof of the mantle-cavity, into which it imperceptibly passes aborally. At its oral end it projects parallel to the axis of the buccal mass— quite free and separated by a deep groove from the hood and tentacle-mass. Tongue-like in form, its margins are inrolled about a longitudinal axis, so that one comes to overlap the other. Which does so appears to be quite inconstant in dif-

ferent individuals, and in any one individual the right and left margins present exactly the same appearance; there being nothing to point to one in particular being kept habitually folded over the other. From this, and from the general muscular character of the funnel, I have little doubt that the living animal possesses the power of unrolling and flattening it out, possibly even of using its broad lower face to creep on or adhere to rocks. In spirit-specimens one can readily so unroll the funnel, and when this is done the appearance of the animal is very striking, as is shown in Pl. IX. fig. 1, where, by the way, the mantle-flap has been partially removed so as to afford a better view of the creature. One is here impressed, first of all, by the sharp way in which the funnel is marked off from the hood-tentacle-head mass. Everywhere a deep groove separates them[1]. There is nothing here to suggest or even support the view that part of the foot has grown up round and become fused with the head. Again, the great size of the organ is very impressive—more especially its width from side to side,—and its entire condition is such as at once, to my mind irresistibly, to suggest that in this organ one has the representative of the whole of the foot of the ordinary Gasteropod.

The general relations of the parts in *Nautilus* impress upon one that :—

> (1)   The hood-tentacle complex is preponderatingly anterior (dorsal) to the buccal mass, its posterior (ventral) parts being relatively insignificant.
>
> (2)   The hood-tentacle complex is most sharply marked off from the funnel by a deep groove.
>
> (3)   The funnel is enough, in itself, to represent the whole of the Gasteropod foot.

Considering merely them alone, there is no suggestion of doubt that the hood-tentacle complex is cephalic; that the funnel is the Gasteropod foot.

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[1] In this connection the figure given by Lankester (*Zoological Articles*, fig. 91) seems scarcely in accord with the actual conditions as shewn in my specimens.

It is because, at the present time, after many years of controversy, the contrary view, which for shortness may be referred to as the 'pedal' view, has gained the ascendency and has come to be the one enunciated by the most authoritative text-books[1] that the present discussion seems necessary.

When Lankester published his *Encyclopædia Britannica* article on Mollusca, he pointed out that the view taught by Leuckart, Huxley, and himself, that the Cephalopod arms are pedal in their nature, was based upon three different sets of evidence—to wit, those derived from

(1) Their ontogenetic development ;
(2) Their innervation ;
(3) Their homology with the sucker-bearing processes of the larval Pneumoderma.

Of these (3) derived its force from the supposed pedal nature of the sucker-bearing appendages. However, it has now been satisfactorily shown[2] that they are purely cephalic, and therefore this argument, if it be argument at all, tells precisely in the opposite direction. At present, therefore, the view that the Cephalopod arms are parts of the foot rests upon (1) and (2). In regard to (1), however, although it must be admitted that the facts of embryology do tend to bear up the view that the crown of arms is formed by an upgrowth from each side of the foot, it must be borne in mind how extremely unreliable any evidence, as to topographical relations, must be which is based on the phenomena exhibited in the development of enormously yolk-laden eggs. Therefore it appears that the only one of the three classes of evidence adduced above which can be considered of real weight, is that resting upon the innervation of the parts under consideration, and that this opinion is shared by other workers, is shown by its tendency in more recent writings to supplant the evidence derived from embryology. It appears, therefore, not inadvisable to submit this portion of the evidence to a short critical examination, to

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[1] Lang's *Lehrbuch*, pp. 587, and Korschelt and Heider, p. 1176.
[2] '*Challenger' Reports:* Pteropoda, Anatomy, p. 39.

endeavour to ascertain whether it is equal to bearing the strain of acting as main support to a view which we have seen to be inherently improbable, on the evidence afforded by gross anatomical relations. And as a preliminary it may be well to look into the general ideas now held and taught by zoologists as to the general character of the Cephalopod central nervous system.

In the latest text-book of Zoology (Lang, p. 722) one reads, "Das symmetrische Nervensystem aller Cephalopoden zeichnet sich durch *die sehr starke Concentration der typischen Mollus-kenganglien*, auch derjenigen der Visceralconnective, aus[1];" and this I think I may venture to say fairly represents the views held and taught by zoologists generally: that the Cephalopod central nervous system consists typically of three pairs of ganglia aggregated round the œsophagus, which ganglia are homologous with the three similar pairs of, say, a Gasteropod. That a certain rough resemblance does exist between the arrangement of the ganglia round the œsophagus of a Dibranchiate Cephalopod and that met with in many Gasteropods may be at once admitted; but when it comes to be a question of precisely homologizing the individual ganglia in the one case with those in the other, one has to do with a very different matter. Supposing, for a moment, the homology to hold, then one ought to find the resemblance most marked in those Cephalopods which phylogenetically most nearly approach the common ancestral forms of Gasteropods. But what are the actual anatomical facts?—that in the *Nautilus*, the most primitive and oldest Cephalopod now existent, such division into three pairs of ganglia is completely absent. And then one might turn to that Gasteropod (I here use the term in its wide sense) which other evidence points to as having similarly to the greatest extent retained such common ancestral conditions—to wit, *Chiton*. And here again one finds a complete absence of segregation of the central nervous system into its three pairs of ganglia, and in its stead a central nervous system showing in

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[1] The italics are mine.

many respects a strong and fundamental resemblance to that of *Nautilus*. The facts of Anatomy, then, are strongly opposed to any rough-and-ready homologizing of the various ganglia of the higher Cephalopod with those of the higher Gasteropod. One might go so far as to say that they demonstrate their non-homology. The common ancestor of Gasteropods and Cephalopods, so far as we can see, possessed, as did and do so many other primitive forms, a nervous system consisting of thick strands ensheathed in a continuous layer of nerve-cells; and any departure from this condition, in the direction of collecting and centralizing these nerve-cells into ganglia to fulfil local requirements, is a process which has taken place independently within each of the two stems of descent.

It follows, from this independence in phylogenetic development of these secondarily formed ganglia, that we are not justified in taking any one of the ganglia of the higher Cephalopods and saying this is the "pedal" ganglion (implying in the term "pedal" accurate homology with the so-named ganglia of Gasteropoda)—*à fortiori*, in asserting here is an organ innervated by the pedal ganglion, therefore it is morphologically part of the foot. Yet it is precisely this latter line of argument which modern exponents of the "pedal" hypothesis use as their mainstay.

The central nervous system of Cephalopoda may be said, according to what we know of *Nautilus*, to consist primarily of—

(1)   A supra-œsophageal mass, connected with
(2)   An anterior sub-œsophageal, and
(3)   A posterior sub-œsophageal mass.

To these is added *in the Dibranchiata* a separate nervous mass lying in front of (2)—the branchial ganglion; and it is this which innervates the arms.

To quote Pelseneer (*Chall. Rept.* p. 65):—

"Regarding (1) there is no disagreement as to its nature, all recognising in it the fused cerebral ganglia.

(2)   "Has been universally regarded as constituted by the pedal ganglia.

(3)   "Corresponds to the combined visceral ganglia of other Mollusca.

"All observers are agreed as to the interpretation of the supra-œsophageal and the two posterior sub-œsophageal masses (*i.e.* (2) and (3)). The disagreement relates only to the branchial ganglia, which are regarded by one party as pedal and by the other as cerebral."

Pelseneer then goes on to combat the view that the branchial ganglion has been derived from the fusion of a downgrowth on each side of the cerebral ganglion.

While protesting, in passing, against the statement that the supra-œsophageal nerve-mass is formed of "the fused cerebral ganglia," when in reality it represents the primitive nerve-mass out of which "cerebral ganglia" have not yet become segregated, it is (2) the statements as to the "pedal" and branchial ganglia which concern most closely the point under discussion. The one fact of independence of evolution is enough to show that the so-called pedal ganglion of Cephalopods—*i.e.* the anterior sub-œsophageal nerve-mass of *Nautilus*, which in the higher Cephalopods has, in accordance with a very general law, become condensed into a definite ganglion, supplying the various organs originally in its neighbourhood—is not in the strict morphological sense the "pedal" ganglion at all. One may then accept with Pelseneer the development of the branchial ganglion by splitting off from this anterior sub-œsophageal nerve-mass, and yet be as completely without evidence as we were before that the structures supplied by it have anything whatever to do with the foot.

In brief it appears to me that:—the general relations of the parts point undoubtingly to the arms of Cephalopods being processes of the head-region—that all the special evidence brought forward to support the pedal view is either erroneous, of little weight, or is permeated with fallacy—and that it therefore behoves us in the meantime to unhesitatingly accept the first mentioned[1].

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[1] The forerunner of the hood-tentacle complex of *Nautilus* (and consequently of the arms of the Dibranchiata) we may probably see still persisting in the similarly innervated and highly sensitive mass which surrounds the mouth in *Chiton*.

IX. The Phylogenetic Relationships of the Cephalopoda.

From its archaic character *Nautilus* might be expected to give valuable hints as to the phylogenetic relationships of the group to which it belongs. Upon the whole it appears to me that its structure affords strong evidence that the nearest living allies of the Cephalopoda are to be found in the Amphineura. And it is interesting to note that amongst these it is the Chitons in which the points of resemblance are most striking, as they are apparently the oldest and most primitive members of the group. The number of really important morphological features in which the Chitons resemble *Nautilus* is quite remarkable, e.g.—

(1) Its bilateral symmetry.

(2) The general characters of its nervous system.

(3) Its possession of paired metamerically arranged ctenidia, of which in some species, believed to be phylogenetically younger, there is a tendency for those at the anterior end of the body to disappear—only those towards the posterior end persisting (*mero-branchiate* forms).

(4) The traces of metamerism exhibited by the heart in some forms, there existing several pairs (four in *Chiton magnificus*) of auriculo-ventricular openings.

(5) General relations of cœlom, nephridia, &c.

(6) Eggs developed within follicles.

In regard to (5), fig. 6 indicates diagrammatically the relationships of the parts concerned. In the case of *Chiton* (B) two cœlomic chambers are shown, one lying in front of the other—the genital cœlom and the pericardium. The pericardium communicates with the exterior by a pair of functional nephridia; the genital cœlom by the pair of genital ducts which from their relations can hardly be otherwise than morphologically a pair of nephridia too. In *Chætoderma* (A), a less primitive animal, a less primitive arrangement has

been developed: the genital division of the cœlom has developed a communication with the pericardium through which the genital products pass—and it has lost its original genital ducts. Fig. C shows the condition in *Nautilus*, where again the same two cœlomic chambers are visible.   Here also a communication

Fig. 6.
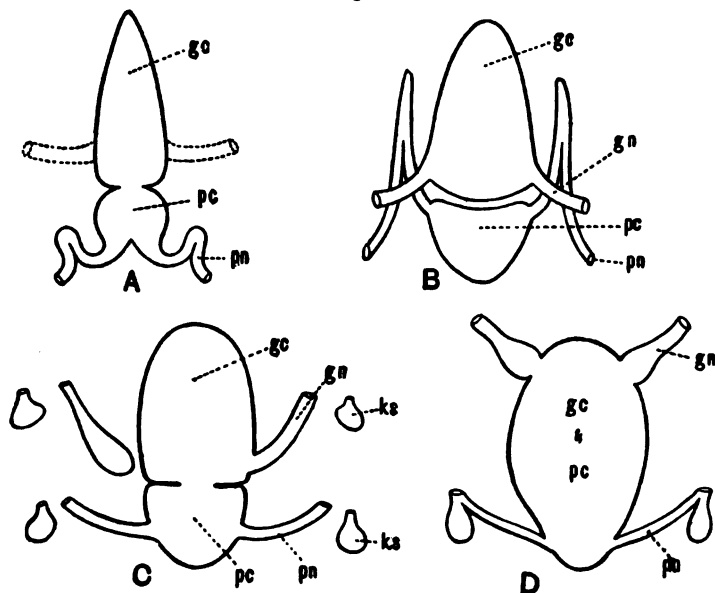
Diagram showing the relationships of the cœlom and nephridia in *Amphineura* and *Cephalopoda*.

A, *Chætoderma;* B, *Chiton;* C, *Nautilus;* D, *Sepia.*

gc, genital division of the cœlom; pc, pericardiac division of the cœlom; gn, nephridia of genital segment; pn, nephridia of pericardiac segment; ks, kidney-sacs in *Nautilus;* in *Sepia* the two posterior kidney-sacs are seen still in communication with the rest of the nephridia.

has become formed between the two, but the two pairs of ducts to the exterior still persist—the anterior nephridium here still preserving its excretory portion—a more primitive condition than in *Chiton*, and probably to be correlated with the fact of its having become shut off from the main lumen of the duct.   A few irregular apertures in the wall separating the two cœlomic

chambers point towards the still later condition to be met with in *Sepia* (D), where the septum has disappeared—a faint rudiment remaining in the form of a transverse fold rising up from the floor of the common chamber[1].

X. SUMMARY OF CONCLUSIONS.

1. The perivisceral cavity in *Nautilus* is remarkable for the almost equal participation in its formation of both coelom and haemocoel.

2. The coelom consists of two distinct chambers—genital and pericardial—separated by a perforated septum.

3. Each of these coelomic chambers opens to the exterior by a pair of nephridia.

4. The genital ducts of the Cephalopoda represent portions of nephridia.

5. The ovary is remarkable for its extremely archaic character—an ovigerous region of the coelomic epithelium, roofed in by a simple upgrowth of the coelomic wall.

6. The ova arise from syncytial masses of protoplasm.

7. The testis is also archaic in character, and similar to the ovary in its main features. Its cavity, however, has become subdivided into numerous delicate tubes for the provision of increased area of the spermatogenetic epithelium.

8. The penis is a paired structure, its left moiety, however, remaining rudimentary.

9. An elaborate buccal nervous system is present.

10. The "inner inferior lobe" is innervated not by a pair of distinct ganglia, but by a continuous nerve-cord.

11. Round the base of the postanal papilla is a curious system of skin-glands.

[1] The view advocated by Grobben (*Morph. Stud.* p. 89) that the condition in *Sepia* is the more primitive, and that it represents a stage in the evolution of the condition met with in the other Mollusca, seems to me untenable.

12. A prolongation backwards of the nerve-trunk which supplies the gills probably represents the postanal commissure of *Amphineura*.

13. A laminated organ lying below the mouth has a function in connection with copulation—the spermatophore of the male becoming attached to it.

14. The evidence as to the "pedal" nature of the Cephalopod arms appears to rest on insecure foundations, and it seems desirable to abandon it for the inherently much more probable view that these structures are processes of the head region.

15. *Nautilus* shows many strong resemblances to the Amphineura, and it is probably amongst these latter that we have to look for the nearest allies of the Cephalopoda.

EXPLANATION OF THE PLATES.

PLATE IX.

Fig. 1. Side view of an animal of *Nautilus pompilius*, extracted from the shell. The funnel has been opened out and the mantle-flap partly cut away so as to give a better view of the various parts.

h, hood; *t*, tentacles; *e*, eye; *f*, funnel separated by a deep groove from the hood-tentacle mass; *m*, cut edge of mantle-flap; *g*, gill; *s*, siphuncle.

Fig. 2. Longitudinal section through the animal of *Nautilus* very slightly to the right of the middle line.

b, buccal cavity; *r*, radula; *cg*, supra-œsophageal nerve-cord; *pl.g*, posterior subœsophageal nerve-cord; *p.g*, anterior ditto; *f*, funnel with its valve; *ph*, crop; *int*, intestine; *an*, anus; *k*, kidney-chamber with follicular appendages of advehent vein projecting into it; *p.foll*, pericardial gland-follicles projecting into pericardium; *v.c*, vena cava.

PLATE X.

Fig. 1.   View of penis and sac of Needham from posterior (ventral) aspect.
The outer wall has been removed so as to show *a* and *b*—the
right and left halves of the penis.

c, sac of Needham; *d*, corresponding structure of left side;
e, bristle passing through opening of vas deferens into sac of
Needham.

Fig. 2.   Spermatophore-receiving apparatus of an adult female with sper-
matophore (*s*) *in situ.*   In this specimen the laminæ of the organ
were continuous across the middle line.

Fig. 3.   The same organ in its more usual (paired) form.
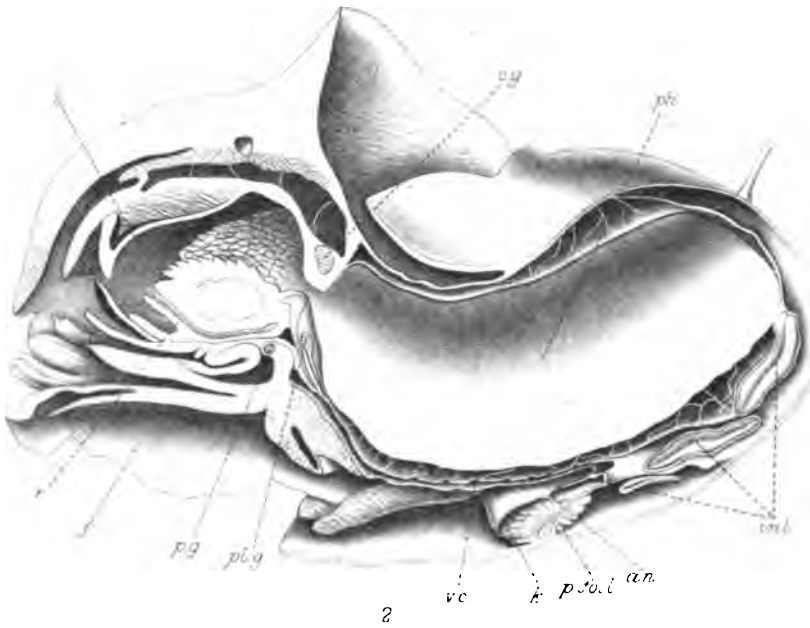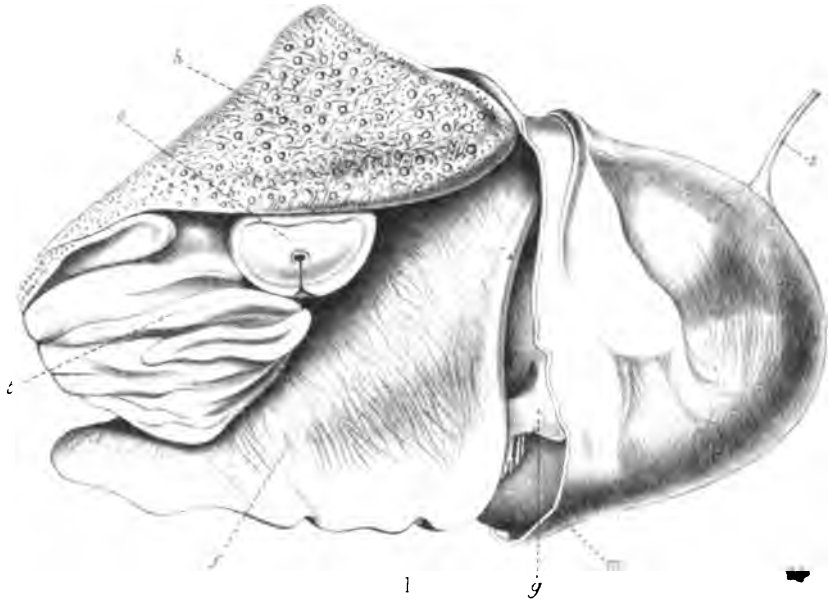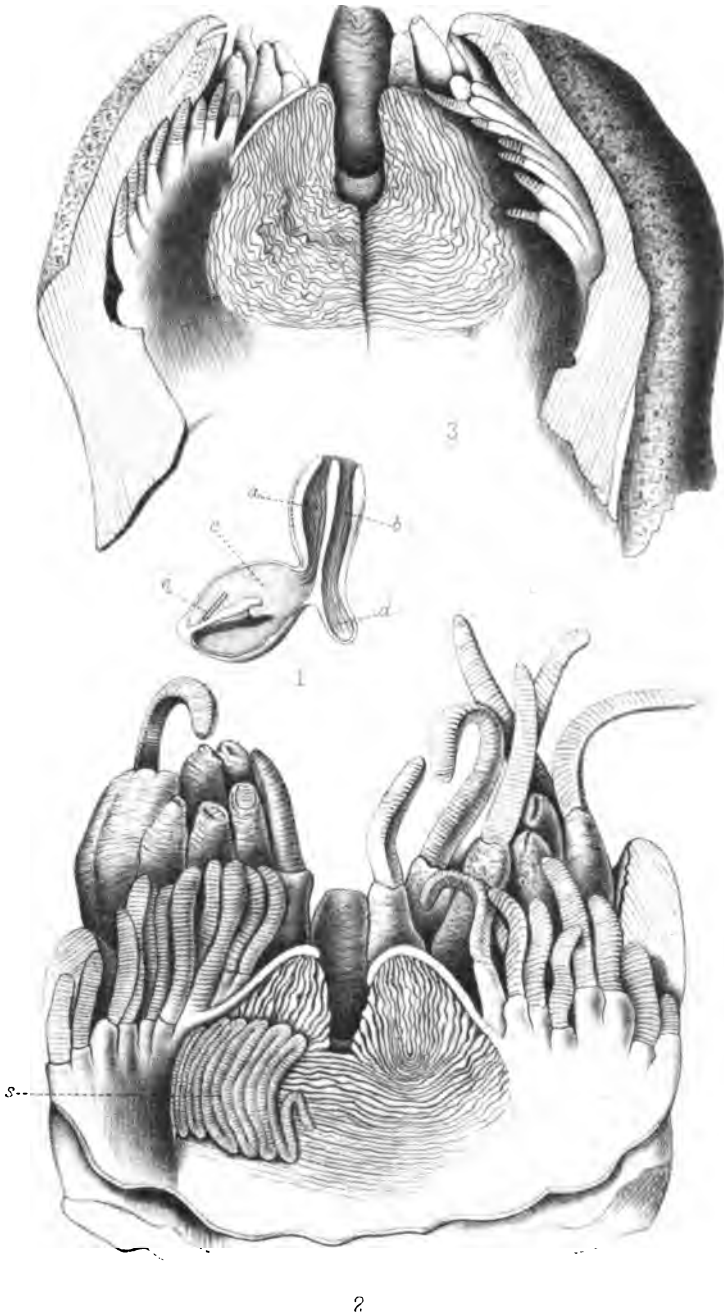
ANATOMY OF NAUTILUS POMPILIUS

ANATOMY OF NAUTILUS POMPILIUS

Further Remarks on the Cell-theory, with a Reply to Mr. Bourne.

By

Adam Sedgwick, F.R.S.

In a paper published last autumn (this Journal, vol. 37), I called attention to the apparent inadequacy of the cell-theory. Recently a criticism upon my article has appeared from the pen of Mr. G. C. Bourne, to which I may be allowed to devote a few words. But before replying to Mr. Bourne, I should like to state my position with regard to the theory a little more fully than I have hitherto done. In my previous communication I used the word "inadequacy" because it seemed to me to express, as nearly as possible, my own views with regard to the theory. A theory to be of any value must explain the whole body of facts with which it deals. If it falls short of this, it must be held to be insufficient or inadequate; and when at the same time it is so masterful as to compel men to look at nature through its eyes, and to twist stubborn and uncomformable facts into accord with its dogmas, then it becomes an instrument of mischief, and deserves condemnation, if only of the mild kind implied by the term inadequate.

The assertion that organisms present a constitution which may be described as cellular is not a theory at at all; it is—having first agreed as to the meaning and use of the word cell—a statement of fact, and no more a theory than is the assertion that sunlight is composed of all the colours of the spectrum. The theory comes in when we try to account for the cellular constitution of organisms; and it is this theoretical part of the cell-theory, and the point of view it makes many

of us assume, that I condemn. It is not the word " cell " which
I am at issue with, for structures most conveniently called
cells undoubtedly exist, as the ovum, spermatozoon, lymph-
cells, &c.; and I fully agree that the phenomenon called cell-
formation is very general in organic life. But at the same
time I hold with Sachs and many others that it is not of
primary significance, but "merely one of the numerous ex-
pressions of the formative forces which reside in all matter."
No one who has studied animal tissues could for one moment
deny that nuclei have in many cases a relation to the
surrounding protoplasm, a relation which is expressed in
the arrangement and structure of that protoplasm. They
have not always this relation, but it is usually present, and
the question is, how are we to interpret it? That we
cannot interpret it finally until we know the relative values of
nucleus and extra-nuclear protoplasm, and the functional re-
lation between the two, is clear; but we may form and hold
provisional theories. The hypothesis or idea which holds the
field at the present day is the cell-theory in its modern form.
This theory, recognising the cellular structure (while not ad-
miring the phrase, I must use it for want of a better one)
asserts that organisms of Metazoa are aggregations or colonies
of individuals called cells, and derived from a single primitive
individual—the ovum—by successive cell-divisions; that the
meaning of this mode of origin is given by the evolution
theory, which allows us to suppose that the ancestor of all
Metazoa was a unicellular Protozoon, and that the develop-
ment of the higher animals is a recapitulation of the develop-
ment of the race. Thus the holoblastic cleavage of the ovum
represents the process by which the ancestral Protozoon be-
came multicellular, and the differentiation of the cells into
groups the beginning of cellular differentiation. According
to this view the order is: unicellular stage—multicellular
stage—differentiation of cells into tissue elements; cellular
structure preceded cell-differentiation, and to get tissues you
must first have cells. And ten years ago it was commonly
held that these cells were primitively separate from one another,

and that the connections found between them in the fully formed tissues were secondary. You had your neuro-epithelial cell, and your musculo-epithelial cell, each derived from a distinct cell produced by division of the ovum; and the question was, how do they find each other and become connected?[1] Further, in studying the development of a tissue you had to find a group of cells, each of which became modified into one tissue element. Thus the primitive streak was a proliferating mass of cells which eventually gave rise to a number of meso-dermal tissues; the nerve-crest similarly was a mass of cells which gave rise to nervous tissues; a nerve-fibre was one of these cells elongated, and before you would get your nerve-cell and fibre you must have your nerve-crest cell produced by division from the cells of the nerve-cord, and subsequently sending out a process which elongated and travelled to the periphery as a nerve-fibre.

My work on Peripatus first led me to doubt the validity of this view of the origin of the Metazoon body. In the first place I found that in some forms there is no complete division of the ovum, and on examining the facts I discovered that such forms were more numerous than had been supposed. It therefore appeared that in some Metazoa the ovum divided into completely separate cells, while in others it did not so divide. The question then arose, which of these methods is primitive? and the answer naturally was, the complete division, because this fitted in with our ideas as to the supposed evolu-tion of the Metazoa from a colonial Protozoon. But on reflection this difficulty arose: the individuals of colonial Protozoa are in protoplasmic connection, while the cells of the completely segmenting ova are separate; so that the parallel between the ontogeny and the phylogeny breaks down in an important particular. To get over this difficulty it was necessary to suppose that the isolation of the segments of incompletely segmenting ova was apparent and not real, that

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[1] For exposition of this view vide Flemming, 'Zell-Substanz, Kern u. Zell-Theilung,' Leipzig, 1882, p. 74, and Balfour's Address to the Depart-ment of Anatomy and Physiology at the British Association in 1880.

they were really connected by protoplasmic strands which had escaped observation. But, on the other hand, there was the possibility that the completely segmenting ova were secondary acquisitions of ontogeny, and that the development in such forms as Peripatus, Alcyonaria, &c., was more primitive, and that the passage from a Protozoon to a Metazoon had taken place by way of a form more resembling a multinucleated cilated Infusorian than Volvox. In other words, that the differentiation of the Metazoa had been effected in a continuous multinucleated plasmatic mass, and that the cellular structure had arisen by the special arrangement of the nuclei in reference to the structural changes. This was the stage to which my researches on Peripatus led me. Since then I have paid attention to Vertebrata, and I have found that a number of embryonic processes have been wrongly described, amongst them such important matters as the development of nerves and the origin of the mesoderm; and I thought that I traced the errors referred to to the dominating influence of the cell-theory in its modern form, for the facts seemed so obvious in themselves that it would have been impossible to make any mistake about them had they been examined without the prejudice imparted by a preconceived theory. A theory which led to such obvious errors must, I thought, be wrong, and I denounced it. But my denunciation in no way implies that I fail to recognise the so-called cellular structure of organisms or their origin from the one-celled ovum. On the contrary, I was led to a reconsideration of the question, what is the meaning of the predominance of the structure called cellular, which is characterised by a definite relation of the nuclei to the functional tissues, and of the fact that the organism so often passes through a unicellular stage. With regard to the former I must say that I have arrived at no conclusions which enable me to formulate to myself any satisfactory hypothesis, and, as I stated at the outset, I do not think it is possible to do this until we acquire some more understanding of the relative function of nuclei and protoplasm. But with regard to the latter there are some facts which might

well be considered. In the first place, the unicellular origin
is only found in sexual reproduction, not in asexual. The
characteristic of the unicellular form is its simplicity of struc-
ture, and the essential feature of sexual reproduction is the
conjugation of the reproductive cells. Now in the Protozoa,
in which the amount of formed tissue is generally slight and
the structure of the body simple, conjugation can and does
often take place between the ordinary form of the species.
But in the Metazoa, in which conjugation is as necessary a
phenomenon in the specific cycle as in Protozoa, conjugation
is impossible between adult or ordinary individuals of a species
from mechanical causes. How is this difficulty got over in
nature ? My answer is, by the formation of special individuals
of extremely simple structure—a structure so simple that conju-
gation between them is possible. To put the matter in another
way, I should regard the ordinary diœcious Metazoon as a tetra-
morphic species, consisting of male, female, ovum, and sper-
matozoon, the two latter being individuals which are specially
produced to enable conjugation to take place.

Mr. Bourne, in his criticism, begins by complaining that he
cannot ascertain from my article my own views on the subject
of the cell-theory. Why should he expect or wish to discover
them ? My remarks were simply directed to show the short-
comings of the theory with regard to certain anatomical facts.
As explained above, my own view is that the cell-theory is
inadequate to explain the facts, and that it is not possible at
present to explain them by any theory. He proceeds to state
that I am abusive because I say that certain observers " are
constrained by this theory with which their minds are saturated,
not only to see things which do not exist, but also to figure
them " (I am referring to embryonic mesoderm of verte-
brates). He calls this abuse, not argument. I venture to
differ with him—it is neither abuse nor argument; it is merely
a statement of fact (unless, indeed, it be considered abusive
to say that a man accepts and believes in the cell-theory). If
you disbelieve it, consult the memoirs of the last twenty years
in which this tissue is referred to, and in most of them you

will find the mesenchyme described or figured as consisting of branched, isolated cells.

Mr. Bourne then refers to certain remarkable researches which emphasize the distinction and complete isolation of the cells formed in the segmentation of the egg; with what object is not apparent, for he proceeds on the next page to condemn those who hold that the organism is constituted of independent and isolated units. He even maintains that no reputable biologist holds such a view. However that may be, I do not think that his quotation from Haeckel in support of his contention is a happy one, for it is perfectly clear from the quotation that Haeckel, who indeed goes so far as to call the units individuals, holds the view which Mr. Bourne condemns.

Haeckel even calls them individuals of the first order, and says that in the adults they frequently unite to form colonies; and he particularly implies that the loss of independence caused by their colonial union is secondary. Mr. Bourne has completely failed to grasp Haeckel's meaning, else how can he write as he does on the same page with the quotation from Haeckel—" So that, as a matter of history, while plants used to be considered to be colonies of independent life units, animals were not."

The most remarkable part of Mr. Bourne's criticism is that in which, after strongly animadverting on my statement that it is difficult if not impossible to enunciate the cell-theory in a manner satisfactory to every one,—indeed he quotes from Schwann and Hertwig to show how precisely it can be stated,—he proceeds to devote a dozen or more pages of his paper to a consideration of the various views which are held and which may be held as to what a cell really is! If this amount of discussion is required to arrive at the meaning of the word cell, is it likely that there will be simple agreement as to the theory which is supposed to explain and account for the so-called cellular constitution of organisms?

Again he says, referring to my description of the embryonic mesoderm as a protoplasmic reticulum with nuclei at their

nodes: "Does he accept the logical consequences of this, and say of the epithelial cells of the salamander or of unstriped muscle fibres, that they are protoplasmic reticula with nuclei at their nodes?"

Now, with all due respect to Mr. Bourne's logical faculties, may I ask him where logic comes in here? If I describe London as a network of streets, with public-houses at many of the street corners, am I obliged by logic to give the same description of the Gog-Magog Hills?

However, on the next page Mr. Bourne makes up for all the hard strictures he has passed upon me; for he says that, after all, reflection may induce us to abandon the cell-republic or colonial theory; thus he admits a very important part of my contention, for the assertion that organisms present a constitution which may be described as cellular is not a theory at all, it is a statement of fact (having agreed to the use of the word cellular). The theory comes in when we try and account for the cellular constitution of organisms; and it is this theoretical part of the cell-theory which I condemn, and which Mr. Bourne after a great effort agrees with me in condemning. At the same time it is possible that we might still disagree as to the meaning of the word cellular.

May I call attention to Mr. Bourne's remarkable faith in the rapidity of evolutionary changes? He says (page 169) that Schwann's assertion that "the elementary parts of all tissues are formed of cells, &c.," is even more true to-day than when it was written. Also I should like to know how he reconciles the implication at the top of page 170, that "specialisation is not possible in continuous tracts of protoplasm," with the statement a few lines further on, that "in the Protozoa there is differentiation within the limits of a single corpuscle."

The criticism on page 172 as to my use of the word empty is not quite fair. On reference to the context it will be seen that the word empty clearly means "empty of structural elements."

The Development of Asterina gibbosa.[1]

By

E. W. MacBride,

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University of Cambridge.

With Plates XI—XXII.

THE investigations which form the subject of the present
memoir were commenced with the object of seeking in Asterids
the results which the author (14) had already obtained from the
study of Ophiurids, viz. the development of the so-called heart
and its accompanying sinuses.

A study of the literature soon led to the conclusion that our
knowledge of the development of most organs in the Asterid body
was very defective, and that a thorough revision of the whole
embryonic and larval history would be most desirable. This
work has occupied my attention for the last two years, and I
am now in a position to give a fairly complete account of the
whole organogeny; an account which will, I hope, place our
knowledge of Asterid development on the same level as that
to which our acquaintance with Crinoid ontogeny has been
raised by the researches of Bury (1) and Seeliger (18) ; I have
to express my warm thanks to Mr. Sedgwick not only for the
suggestion of Asterina gibbosa as a proper type to investi-
gate, but also for much assistance and advice in revising the
proofs of this paper.

That there was an immense lacuna in our knowledge to be

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[1] A preliminary account of the observations recorded in this paper was the
subject of the successful essay in the competition for the Walsingham Medal
of the University of Cambridge in 1893.

filled up will become evident when I state in the first place, that my researches have made it clear that the Crinoids are only very distantly related to the other classes of Echinoderms, and secondly, that our previous knowledge of the metamorphosis of Asterids and their allies was confined principally to the changes which take place in their external form.

It will be most convenient, I think, to give first a general account of the development, and then to point out how far the results of other workers have been confirmed, as by this means needless repetition will be avoided.

Methods adopted.

My material consisted of a large number of larvæ of all stages including those which had just completed the metamorphosis, and of a considerable number of young adults varying from an age of about three weeks to several months from the metamorphosis. Of these the former, with the exception of two small collections made by myself in Plymouth, 1893, and Jersey, 1894, were collected for me and preserved according to my directions by the authorities of the Naples Zoological Station ; the latter were obtained for me and preserved by myself during my stay in the Naples Station in 1892. I have to express my deep sense of my indebtedness to Prof. Dohrn for his kindness in meeting my wishes, and to Cav. Salv. Lo Bianco for the extreme care and attention with which he carried out my directions.

All the stages were preserved in osmic acid, followed by 14—24 hours in Müller's fluid, as this method had yielded me the best results in the case of Ophiurids. It makes the specimens exceedingly brittle, but at the same time gives the most excellent preservation of the minute histology; preserved in this manner the various tissues are differentiated as to their staining capacities, so that the sections look almost like coloured diagrams.

On account of their brittleness, and in order to avoid shrinkage in the tissues, the larvæ were embedded in celloidin, and the celloidin block subsequently embedded in paraffin.

They were then cut into series of sections in most cases $4\frac{1}{2}$ μ thick—in the case of the adults 7 μ; these sections were mounted on hot water on the slide to flatten them, and stained in either Grenacher's hæmatoxylin or Mayer's carmalum. Two points of interest in connection with this process may be mentioned : first, I found that when the slide was transferred from turpentine to absolute alcohol some of the sections were sure to be lost, but that this could be avoided by placing the slide for a minute or so, after taking it out of turpentine, into oil of cloves, and thence into 90 per cent. alcohol; second, that the readiness with which sections, especially when overcharged with osmic acid, will take up either hæmatoxylin or carmalum is greatly increased by immersing them for twenty-four hours in borax-carmine, though they do not acquire a particle of stain from it.

In the youngest stages the osmic acid produces too great impenetrability for either celloidin or paraffin, and accordingly my best results were obtained from some specimens preserved for me by Sig. Lo Bianco in a mixture of three parts concentrated aqueous solution of corrosive sublimate, and one part glacial acetic acid. This method also gives most excellent preservation, though without that fine differentiation of the tissues yielded by osmic acid and Müller's fluid; as during the stages in question however the larvæ consist almost exclusively of epithelial cells, this is not a matter of any importance. This second method was recommended to me by Dr. Eisig.

The orientation of the specimens was one of the chief difficulties to be overcome. I found that the best results were given by horizontal sections perpendicular to the median sagittal plane of the larva, and sections parallel to the disc and perpendicular to the median axis of symmetry in the just metamorphosed star-fish. The planes, to which in these two cases the sections are cut parallel, viz. a median horizontal plane in the larva and the plane of the disc in the adult, make an angle of about 70° with each other; and hence it is difficult to correlate sections cut parallel to the one with those cut parallel to the other. I shall call these planes the "larval"

and "adult" planes respectively. A rudiment of the præoral lobe of the larva is retained, as we shall see, until the close of the metamorphosis, and by means of it I found it possible to determine the direction of the "larval" plane up till the adult form has been almost attained. Hence, by cutting sections parallel to the larval plane, one can follow the internal changes of the metamorphosis step by step; then when the metamorphosis is complete it is possible to correlate with less difficulty sections cut parallel to the two planes, and the further history may be followed viâ, so to speak, the adult plane. This was the course which I adopted; and I also penetrated back a considerable distance from the adult condition into the stages of the metamorphosis by sections parallel to the adult plane, and so confirmed results obtained by the other method. For the youngest stages of all, which are spherical, orientation is, of course, impossible, and one has to trust to chance to getting sections in the proper direction; but it is fairly easy to recognise from their appearance when this is so.

General Account of the Development.

The ontogenetic history of the Asterina gibbosa may be conveniently divided into three parts : first, the development of the bilaterally symmetrical larva from the egg; second, the metamorphosis of this larva into the young star-fish; and lastly, the gradual development of what we may term the young adult into the sexually mature form. I have made no observations on the segmentation of the egg, nor on the gastrulation; my work, properly speaking, commences with the completed gastrula, and my material was not suitable for observing the development of the calcareous plates. On all these points I intend, however, for the sake of completeness, to say a few words, and my authority will be Ludwig, who, in his classic research (12), has on these subjects left nothing to be desired in point of view of completeness. I may add also that the figures illustrating the changes in external form are copied from Ludwig's memoir. The three figures illustrating the relations

of the Asterid and Crinoid to their common ancestor were designed for me by my friend and colleague Mr. J. J. Lister, of St. John's: in their present form they were drawn for me by a lady friend.

The Development of the Larva.

The eggs are laid by the parent on the under surface of stones, to which they adhere by means of their vitelline membrane. I have never discovered a male, though Ludwig says that the male twists his arms round the female whilst she is depositing her ova, and then pours out his spermatozoa upon them; it is quite certain that in the English Channel, at any rate, isolated females will lay eggs which develop with perfect regularity up to the conclusion of the metamorphosis. Cuénot (4) says that young females of a certain size develop spermatozoa in their ovaries—a statement I have not been able to verify. It may, indeed, be said that Ludwig's statement that a kind of sexual congress takes place, Cuénot's observations, and the experience of the authorities of the Jersey Biological Station are irreconcilable, and that the whole subject demands renewed investigation.

The eggs are larger than those of most other Echinoderms; they are about ·5 mm. in diameter. This is a result of the yolk which they contain, and which gives them their bright orange colour. This yolk is so uniformly distributed, however, that it does not alter the type of segmentation, which is total and regular. The blastomeres, in consequence of their larger size, are more closely packed than is usual amongst Echinoderms; they are wedged into the interspaces between their neighbours, and so the strict " radial "[1] type of segmentation characteristic of the group is no longer maintained.

The result of segmentation is a hollow blastosphere or blastula, which on the second day of development becomes converted into a gastrula by embolic invagination. The embryo

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[1] For a discussion of the different types of regular segmentation see " The Cell-lineage of Nereis," by Prof. E. B. Wilson, ' Journal of Morphology,' vol. vi.

is not quite spherical, its long axis exceeding very slightly its transverse axis, so that we can see that the blastopore is situated in the centre of what afterwards becomes the ventral surface. The gastrula has acquired a uniform covering of cilia, and the blastopore is a round opening with well-defined lips. This well-marked stage of development, which is easy to recognise, I have called Stage A (Pl. XI, fig. 1). The blastopore narrows in a peculiar manner, one of its lips becoming reflected over it (Pl. XI, fig. 2), and it is finally reduced to a minute pore (Pl. XI, fig. 3). This opening, which is identical with the larval anus, gradually travels back to near the posterior end of the embryo; this is effected by differences in the rate of growth of surrounding parts. During this time the embryo has been lengthening its long axis, and on the fourth day it ruptures the vitelline membrane and escapes. It then has the form shown in Pl. XI, figs. 4—6, and as this stage is also a well-marked one, I have called it Stage B.

The foregoing is Ludwig's account; my material was not suitable for such observations, which ought to be made on the living embryos, and I had not the opportunity of observing these early stages alive. As far, however, as I could make out, Ludwig is perfectly correct in his statements. I was able to recognise Stage A, for instance, with ease.

Let us turn now to the internal changes which have gone on during this time. Pl. XII, figs. 20 and 21, are two sections of an embryo of Stage A, and they form the starting-point of the changes we shall have to consider ; I may here say at once that all sections which illustrate the development of the larva and its metamorphosis are to be understood to have been cut parallel to the larval plane except the contrary is distinctly affirmed. Fig. 22 is a sagittal section of a slightly older embryo ; here mesenchyme cells have appeared. The large size of the archenteron is a remarkable feature, the blastocœle or segmentation cavity, usually spacious in Echinoderms, being reduced to a mere slit. Fig. 23 shows us that the archenteron becomes differentiated into an anterior thinner-walled vesicle, the cœlom, and a posterior thicker-walled gut;

and in fig. 24 we see that the cœlom has grown back in the form of two tongues, *lpc.*, *rpc.*, lying one at each side of the gut. Fig. 25 shows us a more ventral section passing through the blastopore of the same individual, and we see that in it these cœlomic lobes are absent; they are therefore still confined to the dorsal side of the embryo.

It has been mentioned above that the larva, immediately on escaping from the egg-membrane, has the form of Stage B, and it will be observed that its anterior end has the appearance of being obliquely truncated, and that the anterior surface so constituted is surrounded by a thickened rim, which is covered with specially long cilia, and to which I give the name of **larval organ.** The changes of form involved in acquiring this shape are considerable, and are undergone whilst the larva is still enclosed in the egg-membrane, though superficially the ovoid shape is maintained, the larval organ and the neighbouring ectoderm being to a large extent developed as invaginations into the interior of the larva, exactly as the Tænia head is developed on the wall of the cyst.

The histology of the embryo is illustrated in Plate XIX, figs. 124 and 125. The first is a portion of section of a larva of Stage A, the same specimen as that from which figs. 20 and 21 are taken. Both ectoderm and endoderm are seen to consist of long narrow cylindrical cells, and there is no mesenchyme. Recent researches have gone to show that this is exceptional. Field (5) has proved for Asterias, and it has been long known in the case of Echinids, that mesenchyme is formed by the wall of the blastula before any invagination has taken place. Fig. 125 is taken from a slightly older gastrula. It shows the formation of the mesenchymatous cells by the division of the endoderm cells. I found no indication that mesenchyme continued to be formed when Stage B is reached. The anterior wall of the cœlom is the spot where its formation lasts longest, as in Antedon (18). The cœlomic epithelium consists of small cubical cells (see Pl. XVI, fig. 95).

We must now return to Stage B, up to which we have traced the development. A stomodæum is now developed just behind

the posterior wall and ventral edge of the larval organ. This is well shown in the sagittal section, fig. 31. The larva increases in size, and the præoral portion and larval organ alter their shape, the latter changing from a circular to an elongated elliptical form, whilst the præoral lobe extends in a vertical direction (Pl. XI, figs. 7 to 9). The whole larva has now the form which Ludwig calls slipper-shaped, but which would be more correctly termed boot-shaped, the dorsal lobe of the præoral lobe representing the toe and the ventral one the heel of the boot. In the centre of the larval organ appears an elevation (*fix.*). This structure, which Ludwig did not interpret, we shall find to have a most important function during the metamorphosis; it is, in fact, the disc by means of which the animal fixes itself. Possibly this disc also functions during free life for temporary attachment, though in a different manner; thus when the larval organ is applied to the substratum, the retraction of this disc would cause a cupping action which would be relieved by its again being protruded. It has been pointed out by Ludwig, and I have myself confirmed it again and again, that the larva is able to attach itself most strongly to the substratum. The mode of life of the larva Ludwig calls "creeping." This is not strictly correct; as far as I have seen, the larva swims by means of the cilia of the larval organ. The latter is directed downwards, and for this reason Ludwig calls what I have termed the anterior surface of the animal the ventral, and the posterior end becomes for him the dorsal end. I cannot agree with this orientation; the proper longitudinal axis of any bilaterally symmetrical animal is the oro-anal one, and it is by this that I discriminate between the dorsal and ventral, the anterior and posterior surfaces. That the posterior end is held upwards is no more reason for calling it dorsal than the fact that the Cephalopod directs the apex of its visceral hump backwards is reason for calling that posterior. I should mention that Ludwig calls the whole præoral portion of the body, the præoral lobe in fact, the larval organ. I wish to avoid this, since the præoral lobe has functions which Ludwig did not suspect, and hence I confine the term "larval organ" to the

thickened ridge with long cilia, which is the locomotor organ
of the larva, and is the first thing to disappear in the meta-
morphosis.

Stage C is the point which we have now reached, and it is
characterised by the appearance of this disc for fixation.
Ludwig compares the larval organ to the non-ciliated processes
of the Asterid larva, the Brachiolaria. This larva appears to
be merely a further stage in the development of the well-
known Bipinnaria, from which it differs in the development of
three stalked papillæ from the apex of the præoral lobe, which
are presumably used for attachment. These papillæ arise between
the anterior dorsal and the anterior ventral arms of the Bipin-
naria : one of them is median and more dorsally situated than
the other two, and to this arrangement Ludwig compares the
occasional bifurcation of the ventral lobe of the larval organ of
Asterina. Now, however, that we know the function of the
adhesive disc, it is, in all probability, this which is to be com-
pared to the papillæ of the Brachiolaria; and the larval organ
with its long cilia (compare Pl. XX, figs. 133—135) in all pro-
bability represents some portion of the ciliated bands of the
Bipinnaria. Garstang (6) has, in fact, recently described a
Bipinnaria in which the dorsal arm of the præoral lobe exe-
cutes muscular movements in the same way as Ludwig asserts
for the Asterina larva. I repeat, however, that the latter can
swim by ciliary action alone, without any muscular move-
ment.

The internal changes which have occurred between Stages B
and C are numerous and important. We have already referred
to the appearance of the stomodæum or larval œsophagus.
About the same time the primary madreporic pore is formed;
it arises by a pocket of the cœlom slightly to the left[1] of the
mid-dorsal line, meeting a thickening of the ectoderm (fig.
26, mp.) and a perforation taking place. The pocket of the
cœlom is called the "pore-canal" (pc., fig. 26), and is lined
by cylindrical ciliated cells. By this time the two posterior

[1] This position is not shown in fig. 26; the figure represents a section which
was rather oblique.

lobes of the cœlom have extended so as nearly to meet one another in the mid-ventral line ; the mesentery formed by their apposition is seen in fig. 30, posterior to the gut. The opening of the gut into the cœlom has become closed ventrally (figs. 29 and 30); dorsally, however, it remains open for some considerable time yet. On the left side the cœlom becomes segmented into an anterior portion, a., into which the pore-canal opens, and a left posterior portion, lpc., which we may call the left posterior cœlom (fig. 27); this second cavity includes a large part but not all of the left cœlomic lobe mentioned above; part of this latter is, as is seen in the figure, included in the anterior cœlom. The septum between the two cavities is first formed dorsally, and then extends in a ventral direction; fig. 28 shows it in process of formation.

At the same time one can notice the first indication of that predominance of the organs of the left side which is the key to the whole ontogeny of the star-fish. We see in fig. 30 that the septum between the right and left cœlomic sacs is pushed over to the right, owing to the tendency of the left posterior cœlom to extend over to the right on the ventral side. At no time, so far as I have seen, however, does this septum break down. Some curious trabeculæ are in this stage stretched across the left cœlom. They are easily distinguished from the septum between the two sacs, as they consist of solid strings of cells, whereas the septum has two layers of epithelium with a slit of blastocœle between in this stage. These trabeculæ are very transitory; in figs. 28 and 29 (Stage B) we see them being formed, and in fig. 33 is the last trace of them (Stage C).

As development proceeds the gut becomes more completely separated from the cœlom, the larval anus closes, and the short rectum (fig. 31) disappears. Shortly before this, however, the stomodæum opens into the gut, the main portion of which constitutes the larval stomach (l. stom.), the rectum being very short; but it is only for an extremely short time that the larva possesses both mouth and anus.

Stage C is reached about the end of the fifth day, or the commencement of the sixth day. The division of the left

posterior cœlom from the cœlom of the præoral lobe, which we may now call the **anterior cœlom** (*a.*, figs. 32—35), is complete. On the right side the separation of the posterior part of the right cœlomic lobe, the **right posterior cœlom**, from the anterior cœlom has just commenced dorsally (fig. 32). On the left side the rudiment of the water-vascular system, or, as it is convenient to term it, the **left hydrocœle**, has appeared (as will be related immediately a similar rudiment appears on the right side, but " hydrocœle " alone means left hydrocœle). It originates as an outgrowth from the hinder end of the anterior cœlom ; and whilst it is as yet but faintly marked off from this cavity, indications of its five primary lobes are seen. These are arranged in a curve open anteriorly, and throughout all the figures they are denoted by the Arabic numerals; the most dorsal being No. 1, the most posterior No. 3, and the the most ventral No. 5 (see figs. 32—34). Their mutual relations are well shown in the sagittal section (Pl. XIII, fig. 47), though this represents a somewhat later stage.

We have seen that the division of the right posterior cœlom from the anterior cœlom has begun in exactly the same manner as happened in the case of the left posterior cœlom at an earlier stage. This division has not proceeded very far towards the ventral surface, when the anterior cœlom buds off a vesicle from its right posterior extremity. This vesicle is homologous to the water-vascular rudiment on the left side, for which reason it will be termed the **right hydrocœle** ; so we see that the cœlom on the right side of the larva undergoes exactly the same changes as that on the left, only that they are retarded in their appearance. The first trace of the right hydrocœle is shown in Pl. XVI, fig. 95 ; we see that it consists of a small vesicle of cubical cells arising as a thickening of the cœlomic wall. Its lumen is, in this stage, a minute slit; other preparations show this slit in open communication with the anterior cœlom. It is important to observe that it originates from the dorsal portion of the hinder end of the anterior cœlom, which extends further back ventrally to it, as would be seen if a more ventral section than fig. 95 were shown.

Later stages of this organ are seen in figs. 35 and 36. In fig. 35 it is a conspicuous solid bud; in fig. 36 it has acquired a lumen, and is connected with the anterior cœlom by a string of cells, which soon atrophies, and it is then left as an isolated vesicle in the midst of the mesenchyme. Bury (2), indeed, has seen it in this stage, and called it " a mesenchymatous vesicle ;" and Field (5) has described what I believe to be an homologous structure in the larva of Asterias. The right hydrocœle persists in the adult as a closed sac just under the madreporite, and has been seen here by Cuénot (3), and Leipoldt (9) has described a similar sac in Echinids. It may seem rather a rash assumption to regard this organ as the fellow of the water-vascular system, but a complete proof that this is really its nature will be given when abnormal larvæ are described.

Stage D, the summit of the development of the larva, is reached on the seventh day, according to Ludwig (Pl. XI, figs. 10 and 11). The præoral lobe and the larval organ have greatly increased in size, the former having acquired a large ventral as well as a dorsal lobe. The internal changes are more striking than the external. The separation of gut from cœlom was practically complete in Stage C, the last trace of connection being shown in fig. 36. The right posterior cœlom is entirely separated from the anterior cœlom, but, strange to say, the septum between the left posterior cœlom and the anterior cœlom has become broken down in two places. This occurs by the two layers of epithelium of which it is composed fusing, and then thinning out to a film. Of these two secondary communications between the two sacs, one is situated dorsal to the left hydrocœle (Pl. XIII, fig. 42), and the other ventral to it (Pl. XII, fig. 41). Figs. 42 and 43 belong to the same series; we see that the dorsal opening is formed before the separation of the right posterior cœlom is complete ; the ventral opening is formed at the same time. Not having had the opportunity when I wrote my preliminary account (15) of observing younger larvæ than these, I imagined that the segmentation of the cœlom of the left side was incomplete ab initio, a mistake which was the more excusable as both the breaches in the

septum dividing the two portions of the cœlom from each other become again closed during the metamorphosis.

The left hydrocœle has become much more sharply separated from the anterior cœlom than in the last stage, though in the region of the third lobe the hydrocœle still opens widely into the anterior cœlom (Pl. XII, figs. 38—41; Pl. XIII, figs. 44—46). We saw that the pore-canal in Stage B originated a little to the left of the middle line; now, however, owing to the increasing predominance of the left side, it is shifted to the right of the median plane (*pc.*, fig. 44). The stone canal (*stc.*, figs. 45 and 46) arises as a groove along the anterior face of the transverse septum forming the hinder wall of the anterior cœlom. The central portion of this groove soon becomes closed to form a canal, opening at one end into the hydrocœle between lobes 1 and 2 (fig. 46), and at the other into the anterior cœlom (fig. 45); and this opening is in this stage entirely independent of the opening of the pore-canal.

I have referred more than once to the predominance of the organs of the left side. This is strikingly shown in the stage we are considering by the narrowness of the right posterior cœlom as compared with the left. Already in Stage B we have seen that the left posterior cœlom has begun to sweep round to the right on the ventral side of the right posterior cœlom; this occurs more and more, and in the stage we are considering in the most ventral sections (fig. 41) the right posterior cœlom is entirely absent. The left not only passes under it, but to a certain extent interposes between its anterior portion and the gut (figs. 39 and 40), and here opens freely into the anterior cœlom[1] (fig. 40) by the secondary ventral communication described above. This portion of the left cœlom we may call its right ventral horn; it plays a most important part in the metamorphosis, and it is marked *l'p'c'.* in all the figures.

Ludwig failed entirely to recognise the left posterior cœlom

[1] I may anticipate a little by informing the reader that the anterior cœlom gives rise to the axial sinus of the adult; a space which opens to the exterior by the pore-canal and into the left hydrocœle (water-vascular ring) by the stone-canal.

as a sac separate from the anterior cœlom; he states that the mesentery between the right and left cœlomic lobes is absorbed ventrally. We have seen that only the posterior parts of the right and left cœlomic lobes are employed in the formation of the right and left posterior cœloms respectively; the anterior parts of these lobes are continuous with the anterior cœlom, and the longitudinal mesentery between them breaks down, as Ludwig observed. Hence we see that the hinder part of the anterior cœlom in Asterina is at first a double structure; in the Bipinnaria larva the anterior cœlom is at first double throughout its whole extent.

At the dorsal anterior angle of the left cœlom (fig. 37) an invagination of its wall takes place, giving rise to a thick-walled vesicle (*or. c.*), which communicates by a narrow slit with the cœlom. This structure has been strangely misunderstood. Ludwig saw it, but not its origin, and supposed it to arise as a " schizocœle," and regarded it as the rudiment of the oral blood-ring. In my preliminary account I recognised its true nature, but supposed that its upper end was the rudiment of the so-called heart,[1] with which, as a matter of fact, it has nothing to do. It is the rudiment of the oral cœlom, a space closely surrounding the adult œsophagus, the relations of which we shall study later.

Histology of the Larva.

The structure of the body-wall of the larva is shown in Pl. XX, fig. 138, and Pl. XXI, fig. 144. In the first we see that the peritoneum of the left posterior cœlom consists of

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[1] It will be observed that Bury, in his last paper ('Q. J. M. S.,' September, 1895), makes the same mistake. This work appeared after the present paper had been sent in for publication, and is therefore not referred to further here. The best answer to Bury's criticisms on my observations as recorded in the preliminary account (15) is the publication of full details in the present paper. Bury's observations contain much interesting matter, but also in my opinion many mistakes, which are due to the fact that the stages which he obtained in the development of most of the larvæ he studied, did not form a series without gaps; the orientation which he adopted seems to me also not that which yields the best results.

small cubical cells; the ectoderm is made up of exceedingly long and narrow cells bearing flagella, and the wall of the hydrocœle of similar cells, but I could not make out any flagella there. Fig. 144 is taken from the posterior end of the animal on the right side; the form of the ectoderm cells is well seen, and one observes occasional goblet cells (*gob.*) amongst them. The section goes through a peculiar patch of peritoneum, where the cells are actively engaged in budding off the amœbocytes which float in the cœlom. So far as I can make out, however, no cells are budded off at this stage into the blastocœle (i. e. the space between the ectoderm and the cœlomic wall), and the mesenchyme cells are as yet entirely undifferentiated. The characters of gut cells are shown in Pl. XIX, fig. 126. Although this is taken from a larva in which the metamorphosis has commenced, yet the characters of these cells do not vary till the very close of the metamorphosis. They have the same general form as the ectoderm cells, but the bases of the latter are often contracted, and leave chinks between them, whereas the endoderm cells are closely apposed to one another. Fig. 126 also shows another point of interest: here and there a small round amœbocyte may be seen applied to the basal end of the gut cells, and one discovers amongst the latter also one or two rounded cells, thus suggesting that these amœbocytes may be able to pass between the gut cells like the lymph cells in the Vertebrate intestine.

Plate XX, figs. 133—135, are three sections through the larval organ which have already been alluded to. It is to be noted that in this stage the adhesive disc has short cilia, just as See-liger (18) has described for the adhesive disc of Antedon. Where I have put "*nerv. larv.*" a thin strand of pale fibrous matter is observable with the highest powers. This is the only trace I can discover of a larval nervous system, and I am not perfectly satisfied about it, since it does not take the yellowish-brown tone with osmic acid so characteristic of the adult nervous system. Should my interpretation of it be correct, the larval nervous system would consist of a layer of "Punktsubstanz" underlying the larval organ.

Pl. XX, fig. 137, shows the character of the wall of the præ-oral lobe. The peritoneal cells have developed fine muscular tails (*musc. larv.*), and it is perfectly apparent to anyone looking at sections of a number of larvæ that it is the peritoneum which is the active agent in contraction. The ectoderm is often wrinkled (fig. 38), but the peritoneum never, though its cells vary in shape from cylindrical to flattened according to the state of contraction ; thus in some cases the peritoneal cells on the left side will be cylindrical, those on the right side flattened. The cœlomic wall is in this case short and straight on the one side, and on the other bulged in to the lumen of the anterior cœlom by a great accumulation of the fluid of the blastocœle, or rather (as we must conclude from observations which have been made on other Echinoderms) the blastocœlic semi-fluid jelly. In fig. 137 we see some fine fibrils traversing the blasto-cœle; these, so far as I can make out, are not protoplasmic, but of skeletal nature—of the same nature, that is, as the adult fibrous tissue.

The Metamorphosis.

On the eighth day the larva fixes itself by the adhesive disc by means of a thin secretion of mucilage (see Pl. XX, fig. 136, which represents a much later stage), and remains fixed during the whole of the metamorphosis. I had the opportunity of observing this in Plymouth in 1893 and in Jersey in 1894, and it was most instructive to observe the difference between the larvæ which had thus definitely become sessile and those which, being still able to move, had attached themselves by the cupping action of the muscles of the præ-oral lobe, the larval organ being applied to the substratum.

In the first case, that of truly sessile larvæ, if one attempted to remove them with a pipette, one failed to move them unless very strong suction was applied or they were displaced by a needle; but once displaced they were perfectly helpless, those even which had to all appearance almost completed the meta-morphosis being unable to use their tube-feet (which as yet were rudimentary) ; they could do nothing but feebly rotate by

the action of their general covering of cilia, and they had no
power of re-attachment.   In the case, however, of larvæ which
were attached by what we may call voluntary muscular action,
if one brought the pipette cautiously near so as not to alarm
them, it was very easy to remove them from a stone, just as it
is easy to kick a limpet off a stone if it is taken unawares;
but if they were irritated they were excessively difficult to re-
move, and when one finally succeeded in getting them up into
the pipette, unless one promptly re-expelled them, they at-
tached themselves to the glass, and it was almost impossible to
detach them from it.

The metamorphosis of Echinoderms is probably the most
remarkable ontogenetic change known in the animal king-
dom; but our knowledge of its details has been up to the
present most insufficient.   We possess a completely satis-
factory account of only one form, viz. Antedon, for which the
credit is due to the researches of Bury (1), which have been
amply confirmed by Seeliger (18).   As I mentioned in the
introduction, I hope the account I am about to give of the
metamorphosis of Asterina will compare in completeness with
those I have just mentioned; and as it is of the utmost im-
portance for the comprehension of the meaning of the anato-
mical structure of the Asterid that its relation to the larva
should be thoroughly grasped, I shall anticipate a little what
I have to say in order to make the essence of the process per-
fectly clear.   The metamorphosis of the Asterid, then, consists
in the following processes, which go on simultaneously:

(1) The constriction of the body into disc or body sensu
stricto, and stalk, the latter being formed from the præoral
lobe.

(2) The sharp flexure of the disc on the stalk [the former is
bent obliquely downwards and to the left.   This is not well
shown in any of the figures copied from Ludwig; it is better
seen in the diagram, Pl. XXII, fig. 158 (Dec., 1895)].

(3) The preponderating growth of the organs of the left side,
the left posterior cœlom and the left hydrocœle both sending
out dorsal and ventral horns, which meet so as to form complete

circles, whilst the right hydrocœle and the right posterior cœlom remain small.

(4) The gradual atrophy of the stalk.

(5) The outgrowth of the adult œsophagus and the formation of the new mouth on the left side.

In the Crinoid the list would stand thus:

(1) The constriction of the animal into calyx and stalk.

(2) The displacement of the mouth and neighbouring organs, i. e. the hydrocœle, to the posterior end of the body by unequal growth.

(3) The mutual displacement of the right and left posterior cœloms, the left becoming posterior and the right anterior, both having a ring-shaped growth.

(4) The spiral growth of the intestine and formation of anus close to primary madreporic pore.

It will be seen that the Asterid metamorphosis is very different from that of the Crinoid, being much simpler: one great difference which strikes one at once being that in the former case the ends of the hydrocœle grow so as to embrace the stalk, which thus appears to spring from the oral surface; whereas in the latter case the hydrocœle is carried far away from the stalk to the posterior end of the body. Much diligent search has been made in the centre of the aboral surface of Asterids for traces of a stalk, but to anyone who has grasped the foregoing explanation it will be at once obvious how futile such search must prove. Pl. XXII, figs. 158 and 159, though intended to indicate ancestral forms, illustrate the two metamorphoses outlined above very well.

The sections about to be described illustrating the metamorphosis are nearly all cut parallel to the larval plane, and as was the case with the sections of the larva, where two or three sections from the same series are figured the most dorsal is in every case placed first, and so one can clearly see their relation to corresponding sections of the larva. As one always thinks, however, of the organs of an Asterid as related to the plane of the disc or adult plane, it will be well to repeat the relation which these two planes bear to one another. The

adult plane makes an angle of about 70° or more with the
larval plane; but without any very serious error, it may be
regarded, for purposes of description, as at right angles to it:
thus the direction right to left, according to the larval plane,
becomes aboral to oral according to the adult plane, and dorsal
to ventral according to the larval plane is nearly parallel to
the adult plane.   Here I may remark that the words "dorsal"
and "ventral" will only be used with reference to the larval
plane; in speaking of the adult plane the words "oral" and
"aboral" will be used.

Pl. XI, figs. 12 and 13, show the appearance of a larva which
has only been fixed for a short time.   On the left side we see
that the hydrocœle lobes have become visible externally, since
they have raised the ectoderm into protrusions which, as we
shall find, are the rudiments of sensory terminal tentacles of
the radial water-vascular canals.   Outside the curve of these
rudiments is another set of protrusions, also arranged in an
open curve.   These are the rudiments of the arms: they are
all, as we shall see, outgrowths of the left posterior cœlom, and
their primary function is to form supports for the lobes of the
hydrocœle, to which they later become apposed.   The con-
striction of the præoral lobe or stalk from the body proper is
hardly as yet marked, but the rounded appearance of the dorsal
and ventral outgrowths of the præoral lobe is to be noticed.
This is due to the disappearance of the larval organ, the opposite
sides of which become approximated to each other and wrinkled,
and then broken up, portions of the organ becoming invaginated
into the interior and destroyed by histolysis.   The appearance
of the remnants of it at this stage gave Ludwig the impression
that one had to do with the outgrowth of a series of protrusions
homologous to the adhesive disc.   This is, of course, a mistake;
the adhesive disc remains single and unaltered to the end of
the metamorphosis.   This well-marked phase of development
we may call Stage E.   Pl. XIII, figs. 48 to 50, are taken from
a larva of this age; fig. 48 is of course the most dorsal section
(see explanation of plates).   In fig. 50 we notice the great
growth of the left hydrocœle, lobe 3 reaching nearly to the

posterior end of the body, and we can also make out an arm rudiment, which at this stage is a mere protrusion of ectoderm filled with mesenchyme cells; it forms the extreme posterior end of the section. The rudiment of the adult œsophagus *a. œ* is also seen, and we notice the relation of the oral cœlom to it, and we may remark that the larval œsophagus is by this time disrupted from the gut. Fig. 49 shows that dorsally the hydrocœle is completely shut off from the anterior cœlom, and shows that the oral cœlom dorsally opens into the left posterior cœlom. Fig. 48 shows that the opening of the oral cœlom is in close relation to a process of the left posterior cœlom extending over to the right, dorsal to the gut. This is the **right dorsal horn** (see p. 233 for the ventral horn) of the left posterior cœlom, and it is marked *l″p″c″* in all the figures. In later stages it extends ventrally for a short way, insinuating itself between the gut and the septum dividing the anterior cœlom from the left posterior one (Pl. XIV, fig. 61). The opening of the oral cœlom is later shifted so as to be connected only with the right dorsal horn, and hence it came to pass that Ludwig regarded oral cœlom and right dorsal horn of the left cœlom as one structure, and described the oral cœlom as the oral blood-ring and the dorsal horn as the " heart." In common with all other growing spaces in the larvæ, this right dorsal horn has at its growing tip an epithelial thickening, and it was this which in my preliminary account I mistook for the rudiment of the " heart."

Figs. 51—53, taken from a slightly older larva, show the appearance of the rudiments of the perihæmal spaces. It may be useful to refresh our memory of the arrangement of these spaces in the adult; this the annexed woodcut is intended to do. They are usually described as consisting of a canal situated just aboral to each radial nerve, and divided by a longitudinal septum (Pl. XXII, fig. 155). These radial canals open into a circular canal surrounding the mouth, inside which is another inner ring-canal. The longitudinal septa of the radial canals are inserted into the septum separating these two ring-canals. Into the inner of the circular canals a vertical canal opens

which is the axial sinus, embedded in the wall of which is
the stone-canal (Pl. XVIII, figs. 110—118).   This axial sinus

FIG. 1.
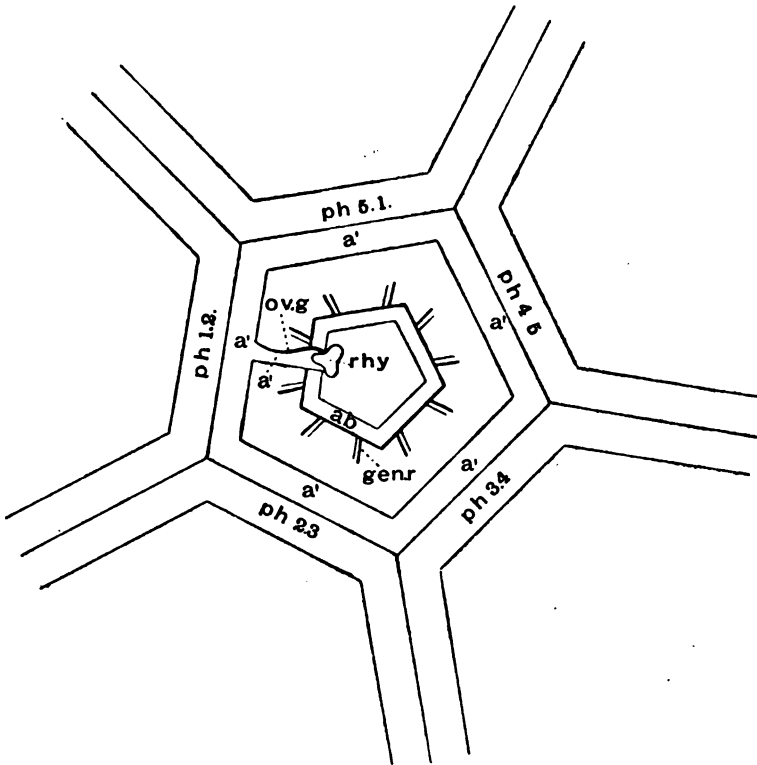
ph. 1.2, &c. Rudiments of the outer perihæmal ring. *a'.* Axial sinus and
    its outgrowth the inner perihæmal ring. *ab.* Aboral sinus. *gen.r.*
    Genital rachis.

was supposed to open at its upper end into an aboral perihæmal
ring or pentagon, from which in each interradius two canals
branched off to go to the genital organs.   As is well known,
these spaces were called "perihæmal" by Ludwig (10), because
he imagined that he had discovered the true blood-system in
the form of curious tracts of tissue embedded in the longitudinal
septa of the radial canals, and in the septum separating the
two circular canals.   He further supposed that that curious

so-called heart, which projects along with the stone-canal into the axial sinus, was connected with this system, and that a string of tissue lying in the aboral ring and connected with the "heart" was also part of the vascular system. We shall, however, see later that these two latter structures ("heart" and aboral string) are of totally different nature from the oral ring, being composed of primitive germ-cells, and have, as a matter of fact, no connection with it. The radial tracts are absent in Asterina, but the oral circular tract is well represented, and we shall study its development later.

The woodcut (p. 241) shows us that the foregoing description is not quite correct. In the first place, we see that one can hardly speak of an outer perihæmal ring, because this space is broken up into five compartments by the prolongations of the longitudinal septa of the radial canals; secondly, apart from the mistake we just pointed out in reference to the nature of the "heart" and aboral ring, we see that the axial sinus (a') does not open into the perihæmal aboral ring; and, further, that to the upper end of the axial sinus is closely apposed a small closed sac, the right hydrocœle.

Returning to figs. 51—53, we see that each of the five compartments of the outer oral perihæmal ring arises separately as a wedge-shaped outgrowth of the cœlom. I have numbered these rudiments according to the numbers of the lobes of the hydrocœle between which they occur—*ph.* 1.2, *ph.* 2.3, *ph.* 3.4, *ph.* 4.5, and *ph.* 5.1; the last, however, arises later, and is not seen in these figures, and the first is an outgrowth of the anterior cœlom (Pl. XIII, fig. 51, Pl. XIV, fig. 54): all the rest arise from the left posterior cœlom. The shape and relations of these rudiments are well shown in the enlarged drawing given of one of them (Pl. XX, fig. 139); we see that the base of the wedge is directed outwards, and that its basal angles tend to insinuate themselves between the ectoderm and the hydrocœle. As a matter of fact, each angle grows out till it meets the adjacent one of the next rudiment. The two then become apposed to each other, and their walls, which meet, form the longitudinal septum of the radial canal, and

both spaces grow out together underneath the growing lobe of the hydrocœle, and thus the radial perihæmal canal itself is formed; we shall find later that the inner perihæmal ring arises as an outgrowth from the oral end of the axial sinus or anterior cœlom, and hence it is marked *a′* in the woodcut.

Fig. 53 shows us that the fourth and fifth lobes of the hydrocœle have extended over to the right; this being the result of the tendency of the two ends of the hydrocœle, which have become entirely shut off from the anterior cœlom, to approach one another. We also see from the obliquity of the right posterior cœlom (compare figs. 44—46 with figs. 52 and 53) · that the lateral flexure of the body on the stalk has commenced. The flexure in a downward direction cannot be well shown by sections.

Pl. XXII, figs. 54—57, are sections of a larva rather older than Stage E. We see that the differentiation of the stalk from the body has been initiated by the dorsal constriction of the neck of the præoral lobe. In consequence of this the anterior cœlom becomes divided into a stalk portion *a*, and a body portion *a′*, the latter forming the axial sinus. We see, further, that the ventral horn of the left posterior cœlom *l′p′c′* has pursued its growth, extending obliquely to the right under the gut, and then upwards in a dorsal and anterior direction, and on its course the last of the five arm rudiments appears, viz. V. Fig. 57 shows the outgrowth of septa destined shortly to close the ventral communication between this right horn of the left posterior cœlom and the anterior cœlom. The primary lobes of the hydrocœle have each by this time given rise to two lateral lobes, the rudiments of the first tube-feet, the primary ones themselves being destined to form the terminal tentacles of the water-vascular system.

Figs. 58 and 59 represent a larva about midway between Stages E and F. We see the final division of the hydrocœle from the anterior cœlom, the last connection being in the neighbourhood of lobe 3, and also the separation .of the axial sinus from the stalk cœlom. We see also the remains of the larval œsophagus (*lœ*.), which already in Stage E has broken off

from connection with the gut; the relative position of the adult œsophagus (*a.œ.*) is also well shown. Fig. 60 is from a larva of about the same age; it shows the formation of the fifth perihæmal rudiment (*ph.* 5.1) as an outgrowth of the ventral horn of the posterior cœlom : this lies beyond the fifth hydrocœle lobe, and will therefore come to lie between this and No. 1 lobe when the two ends of the hydrocœle meet. We also see the process of destruction of the stalk going on, the ectoderm of its anterior surface being invaginated in patches, and, as we shall see, each patch as it is invaginated becomes destroyed by histolysis. Fig. 61 is from a larva which has nearly attained Stage F; it shows how the dorsal horn (*l″p″c″*) of the left posterior cœlom wedges itself in between the gut and the hinder wall of the anterior cœlom (*a′*). In this wall we see running from left to right (i. e. from oral to aboral sides of the disc) from the second lobe of the hydrocœle, the stone-canal. The ciliated cylindrical epithelium of this has now become continuous with that of the pore-canal, but only on one side; the conjoined tubes still open to the anterior cœlom, and this opening persists in the adult, a fact which Ludwig did not observe (to see this, a more dorsal section than fig. 61 would have to be shown). The reader will remember that the pore-canal is formed by a dorsally directed outgrowth of the anterior cœlom fusing with the ectoderm, and a perforation occurring at the point of contact, and that the stone-canal is at first a ciliated groove running along the posterior wall of the anterior cœlom. This groove we found became converted into a canal opening into the hydrocœle on one side, and the anterior cœlom on the other just below the inner opening of the pore-canal (woodcut 2).

We have now arrived at Stage F, the external appearance of which is shown in Pl. XI, figs. 14—16. We notice that the præoral lobe or stalk has become very much reduced, and that the two ends of both curves, that of the hydrocœle lobes (numbered in Arabic figures) and that of the arm rudiments (numbered in Roman numerals), have become very much approximated to each other.

At the same time we see that oral and aboral parts of the

future star-fish are decidedly oblique to one another, being closely apposed posteriorly, but anteriorly separated by the thick base of the stalk. We see also that a lateral shift of the arm rudiments has commenced, No. V having passed beyond the hydrocœle lobe No. 5, and so also in the case of the others. A second pair of rudiments of tube-feet has grown out from each lobe of the hydrocœle, so that they are now 5-partite.

Figs. 62—69, Pl. XIV, are taken from a most instructive series of sections of a larva of this age, and are intended to give a clear conception of its internal anatomy. We are struck at once by the great reduction of the stalk, although ventrally (fig. 66) the stalk cœlom still communicates with the axial sinus. In fig. 65 we see the last trace of the secondary ventral communication between the left posterior cœlom ($l'p'c'$) and the axial sinus a' (anterior cœlom) just closing. The secondary dorsal opening persists much longer, but fig. 63 shows us that it also is beginning to be closed. Comparing figs. 64 and 65, we see that the adult œsophagus has acquired two lateral outgrowths, one directed anteriorly, the other posteriorly; there is also a third horn directed dorsally, which of course cannot be seen in the sections. Fig. 67 shows how the oral cœlom (or.c.) now half encircles the adult œsophagus. As to the arm rudiments, the most interesting thing is to notice the wide separation of No. V from the hydrocœle lobe No. 1. When the intervening tissue shrinks, a change which involves a reduction in size of the axial sinus (compare a'., Pl. XV, figs. 75 and 76), the metamorphosis will be complete. The incipient shift of the other rudiments is seen, especially in the case of Nos. II and III, the latter falling between lobes 3 and 4.

By a continuation of the processes referred to above, viz. the constriction of the base of the stalk, the increasing flexure of the body on it, and the continued growth of the hydrocœle and left posterior cœlom, we soon reach Stage G, which is represented in Pl. XI, figs. 17 and 18. We notice the great reduction of the stalk (which is now usually directed downwards almost at right angles to the disc, though the extent of the angle between the two varies) and the completion

of the circle of arm rudiments, though No. I is not quite
adjusted to hydrocœle lobe No. 2, and the hydrocœle ring is as
yet incomplete.   Here is a fitting place to give in a word or
two the gist of Ludwig's observations on the calcareous plates.
On the oral side (fig. 17) we notice ten small calcareous stars,
two at the base of each primary hydrocœle lobe, situated on
the inner side of the first pair of tube-feet rudiments.   These
are the beginnings of the first ambulacral ossicles (*amb*.).
On the aboral side we notice eleven plates, one central (*C*.), five
situated in the arm rudiments and destined to form the
terminals (*T*.) (the plates which protect the terminal tentacles
of the water vascular system), and five interradially situated,
the basals (*B*.), one of which becomes the madreporite.   The
name "basal" is given on account of an imagined homology
with the basals of Crinoids ; the groundlessness of this assump-
tion I shall point out later.   All these plates make their first
appearance simultaneously, rather earlier than Stage F.   Fig.
19 shows the aboral surface of a young star-fish about sixteen
days old.   We see that the anus has been formed close to the
central; that a plate has been interposed between each terminal
and the central, the former maintaining its position in the
tip of the growing arm, and that finally a pair of plates has
appeared in each interradius, peripherally situated with regard
to the basals, the latter retaining their position in the centre of
the disc.   These paired interradial plates are homologised by
Ludwig with the interambulacrals of Echinids.

Plate XV, figs. 70 and 71, are two sections of a larva of Stage
G.   As in all the figures the stalk is placed as nearly as
possible in the same position, one can see at a glance the very
great lateral flexure which the disc has undergone with reference
to the stalk.   We see the relation of the rudimentary larval
œsophagus to the permanent one ; we further see that the oral
cœlom is commencing ventrally to open into the left posterior
one (this is of course a secondary communication, and I may
say at once that the oral cœlom does not give rise to a separate
space in the adult, but merely forms the part of the cœlom
abutting on the inner side of the buccal membrane), and finally

we observe the incipient bifurcation of the posterior end of the
pyloric sac (which is formed from the larval stomach) to form
the pyloric cæca.

Fig. 79 is a section parallel to the adult plane of a slightly
younger larva; it shows beautifully the mutual relations of the
water-vascular ring (*wvr*), the axial sinus, and the oral cœlom.
If one compares this figure with Pl. IV, fig. 53, in Ludwig's
paper, one sees at once that his supposed rudiment of the oral
blood-ring is only the oral cœlom.   Figs. 75 and 76 show the
completion of the metamorphosis by the apposition of arm
rudiment No. V covering the tip of the ventral horn of the left
cœlom (*l'p'c'*) to hydrocœle lobe No. 1.   As compared with
the larva represented in Pl. XIV, figs. 62—69, we notice the
much smaller size of the axial sinus (*a'*).   Fig. 75 shows also the
bifurcation of the anterior end of the pyloric sac into two cæca.
Comparing it with fig. 76, which is a more ventral section
from a larva of the same age, we see also that the spaces
between the pyloric cæca (*py*) and the aboral body-
wall are continuations of the right posterior cœlom.

Fig. 76 shows also the first trace of ovoid gland ("heart")
(*ov.g.*) arising as a ridge of epithelium including blastocœlic
jelly and fibres and amœbocytes, projecting into the axial sinus.
By comparing this figure with Pl. XIV, fig. 61, the shift of arm
rudiment No. V can be clearly made out.   Figs. 80 and 81 are
sections parallel to the disc of a larva rather older than Stage G.
Fig. 80 shows how the oral cœlom almost surrounds the œso-
phagus, and also that the axial sinus is commencing to form
the inner perihæmal ring by growth from its lower end (compare
woodcut).   In fig. 81 we see at the point marked * the closing of
the water-vascular ring by outgrowths from the hydrocœle lobes
Nos. 1 and 5 respectively.   We also notice what we have already
seen in fig. 76, that the septum between the oral cœlom and the
left posterior cœlom is breaking down; and in fig. 82, which is
from a young star-fish in which the metamorphosis is just
complete, we see that from the remnants of this septum the
retractor muscles of the œsophagus or "stomach" are formed.
The remaining figures on the plate show the finishing touches

of the metamorphosis. In fig. 72 the adult mouth is formed, and the sessile mode of life has been given up, the stalk being reduced to a small solid rudiment. We see also the first trace of the eye as a small knob at the base of hydrocœle lobe No. 3. Fig. 78 shows the permanent anus; if we compare its position with that which the larval anus occupied, we find that they are by no means the same: the larval anus, if it had persisted, would be situated at the point ×, though both occupy a position on the mesentery dividing the left from the right posterior cœloms. Fig. 77 from the same larva shows that the left posterior cœlom now forms a complete ring by the breaking down of the partition between its right ventral and right dorsal horns ($l'p'c'$. and $l''p''c''$.).

In fig. 73 a dorsal section, and in fig. 74 a ventral section, we see the incipient bifurcation of the right posterior cœlom in order to form the outgrowths connected with the two dorsal and the ventral pyloric cæca respectively. We see, therefore, that of the five pyloric cæca, two are formed from the dorsal end of the pyloric sac or larval stomach, and two from its ventral end, and that their suspensory mesenteries are outgrowths from the mesentery separating right and left posterior cœloms. The fifth cæcum is directed dorsally and posteriorly. In Pl. XV, fig. 82, and Pl. XVI, figs. 83, 84, we have three sections parallel to the adult plane of a specimen which had just completed the metamorphosis. Once the mouth is open, the trifid form of the adult œsophagus changes, we get the five slightly bifid lobes of the adult " stomach." In fig. 83 we see the first trace also of the bifurcation of the pyloric cæca; I remind the reader that in each arm of the adult there are two cæca; the characteristic appearance of the axial sinus, stone-canal, and right hydrocœle in a section parallel to the disc are also shown, the right hydrocœle having a crescentic form. Fig. 84 shows us the relation of the rectum and the rudiment of the rectal cæcum to the pyloric cæca; we see that the mesentery which binds the bases of the pyloric cæca together is only the original mesentery between the right and left posterior (oral and aboral cœloms); and, further, that the mesenteric band connecting the inter-

radius of the stone-canal with the stomach is a part of this same original mesentery, with which, however, is continuous a piece of the wall between dorsal and ventral horns of the left cœlom, these two horns being still separated by this wall near their right sides (aboral surfaces).

Histological Changes during the Metamorphosis.

Up to Stage G the histology has little changed from that of the larva before metamorphosis. The most striking alterations are those connected with the destruction of the præoral lobe. Pl. XX, fig. 136, gives a specimen of them. This figure, which is taken from the larva represented in figs. 62—69, shows that the ectoderm becomes invaginated into pockets, and then these pockets completely closed, so that no breach in the continuity of the skin is made. The invaginated portion is then destroyed by amœbocytes as shown in the figure. The peritoneum lining the stalk cœlom contracts violently, the cells becoming cylindrical instead of flattened, and the larval muscles very apparent. So far as I can make out, these cells are destroyed by amœbocytes of the cœlom.

In the larva the whole hydrocœle rudiment is lined by cylindrical cells (Pl. XX, fig. 138); but as metamorphosis proceeds, and the hydrocœle increases in size, the cells are stretched so as to become flattened (Pl. XX, fig. 139); they retain their original character only in the rudiments of the tube-feet (Pl. XXI, fig. 149) and terminal tentacles. The first trace of the adult nervous system appears in Stage F in the ectoderm covering the water-vascular ring,—that is, the portion of the hydrocœle between the primary lobes. The ectodermal cells become long and filamentous, with their nuclei set at different levels, and amongst their bases (Pl. XXI, fig. 140) appears a tangle of fine fibrils of excessive tenuity, so that the highest magnification is required to make them out; this is the first trace of the adult nervous system.

Ludwig talks of cells stretched parallel to the surface under the ectoderm, which he supposed to become the bipolar ganglion cells of the nerve-cord; but the cells in question, if I

rightly identify what he means, are only the epithelial lining
of the perihæmal spaces which at a later period become closely
apposed to the ectoderm. The first trace of muscles in the
body-wall appears much earlier. Pl. XXI, fig. 145, shows the
formation of a well-marked muscular band from the wall of
the right posterior cœlom of a larva of Stage E. We see that
it consists of indubitable myo-epithelial cells. I have traced
this band into the oldest specimen I have examined for histo-
logy; and so far as I can see it appears to become a dilator
of the anus. It is very strange that it should appear long
before any other muscles of the body-wall; it forms quite a
conspicuous feature in sections of all well-preserved metamor-
phosing larvæ. The same figure shows the first trace of histo-
logical differentiation in the mesenchyme; we see the first
formation of that fibrous intra-cellular substance which gives
firmness and tenacity to the adult body-wall.

The cells of the gut remain unchanged till the very end of
the metamorphosis, but in Stage G we can trace some differen-
tiation. Pl. XIX, figs. 127, 128, show part of the lining of the
adult œsophagus and of the pyloric sac of such a larva. The
cells of the former are very long and narrow, and their outer
portions take a clear yellow tone with osmic acid; those of the
latter are ordinary cylindrical epithelium cells.

Abnormal Larvæ.

I mentioned above that the demonstrative proof that the sac
I have termed the right hydrocœle is of that nature is obtained
from the study of abnormal larvæ. I suppose that about one
in thirty of the larvæ I examined were abnormal, though in very
different degrees. The commonest abnormality results from
the unusually great development of the organs of the right
side, and the consequent checking of the metamorphosis.[1] The
larva of which the two sections are given in figs. 85 and 86
had about attained Stage D. The left hydrocœle is perfectly
normal, but the right, though not much larger than usual, is

[1] The reader will remember that in the analysis of the metamorphosis which
I have given on p. 355, one of the main factors recognised is "the preponde-
rating growth of the organs of the left side."

divided into distinct rounded lobes lined by cylindrical epithelium (*rhy.*), in all respects similar to those of the left, and the rudiment opens by a narrow but distinct slit into the anterior cœlom. This larva also exhibits another very common abnormality, which I do not in the least understand; this consists of the breaking up of the gut epithelium into a mass of cells having the appearance of mesenchyme, which choke up the lumen, but leave the walls almost denuded of epithelium, consisting chiefly of the basement membrane. This curious change can take place at any stage from the commencement of the differentiation of the cœlom, up to young adults a month old: in one such specimen it affected the pyloric cæca. As to what its meaning is, I confess I am entirely in the dark.

Figs. 87 and 88 represent a most remarkable larva. The development of the left posterior cœlom would indicate that it had reached Stage E, but the left hydrocœle consists only of four lobes, and is poorly developed. There are two rudiments of a hydrocœle on the right side; the more ventral has three distinct lobes lined by cylindrical epithelium (*r'hy'.*, fig. 88), and opens by a distinct opening into the anterior cœlom; the more dorsal is perfectly normal (*rhy.*, fig. 87); but, as if to emphasise the fact that, in spite of the presence of the other rudiment, it does in fact represent a hydrocœle, we find in connection with it a second small stone-canal and pore-canal (*p'c'. st'. c.*). The relation of these to the right hydrocœle may seem unusual; instead of the canal (conjoined stone and pore-canal) leading from the hydrocœle to the anterior cœlom and thence to the exterior, it appears to lead from the anterior cœlom to the hydrocœle and thence to the exterior. This apparent difference may be reconciled with the arrangement on the left side by observing the angle which stone-canal and pore-canal make with one another. Woodcut 3, p. 252, shows that this is an acute instead of an obtuse angle, and hence that stone-canal and pore-canal have coalesced laterally; Woodcut 2 shows for the sake of comparison the normal stone-canal and pore-canal and their relationship to the left hydrocœle and the axial sinus or anterior cœlom.

Fig. 89 is a section of a larva of Stage D; both hydrocœles
are well developed—the right, in fact, better than the left; the
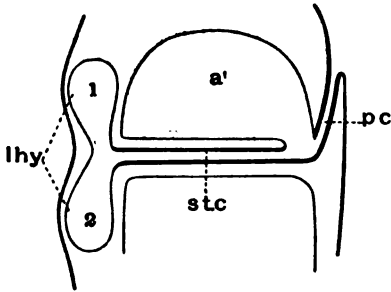
FIG. 2.   FIG. 3.
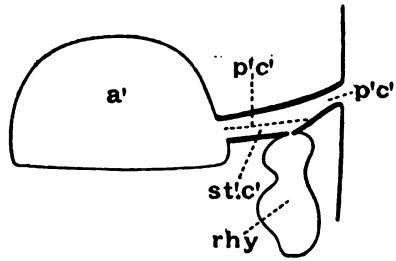
right hydrocœle appears on the left side of the figure, since by
an oversight the section was drawn from the wrong aspect. It
took me some time in this larva to determine which side was
which, but the right hydrocœle is rather more dorsally situated,
and opens by only a narrow slit into the anterior cœlom. It is
also curved somewhat differently, the most posterior lobe being
No. 4, not No. 3, as on the left side. Fig. 90 shows a most
remarkable variation. We see a pore opening directly from the
hydrocœle to the exterior. If, as I shall attempt to show later,
the anterior cœlom may be compared to the proboscis cavity of
Balanoglossus, and the two hydrocœles to the collar cavities of
that animal, we see that what we may term a collar-pore may
arise as a variation. Figs. 91—94 are sections taken from a
larva of Stage G. Its only abnormality is that in connection
with the right hydrocœle, which is of normal character, a
second pore-canal and stone-canal are developed. Fig. 92
should show the opening of the second stone-canal into
the hydrocœle; fig. 93 the opening of conjoined pore-canal
and stone-canal (compare woodcut 3) into the axial sinus.
Fig. 91 shows that the two pore-canals unite, to open by a
common median pore. The above are not by any means all
the variations observed, but they are sufficiently typical to in-
dicate their nature.

The History of the Young Star-fish.

The just metamorphosed Asterina gibbosa has a disc of about ·6 millimetre in diameter; if we take R to denote the length from the tip of the arm to the centre of the disc, then R equals ·36 millimetre.   A larva such as that figured in figs. 51—53 may be ·8 millimetre from the tip of the adhesive disc to the posterior end, and measured obliquely from the dorsal end of the præoral lobe may exceed a millimetre in length.   There is, therefore, a considerable diminution in size during the metamorphosis, the reason of which is evident when we consider that no nutriment is taken during this time.   A full-grown specimen may have a diameter one hundred times greater than that of the just metamorphosed star-fish,—that is, it may exceed the latter one million times in bulk.   The young star-fish, however, rapidly increases in size, and by the time R equals 3·7 millimetres the ovaries are visible.   This is the oldest stage I have examined; my account of the histology is, however, taken from smaller specimens, in which R equals ·8 mm.

The changes we shall have to consider are (1) the formation of the primitive germ cells, the ovoid gland, genital rachis, and ovaries; (2) the dermal branchiæ; and (3) general histological differentiation.

We have already in Fig. 76 seen the first trace of the ovoid gland.   It there appears as a ridge projecting into the axial sinus; inside this ridge there is as yet to be found only amœbocytes, jelly and fibres, as is the case with the other blastocœlic spaces in the larva.   Later, a thickening of peritoneum takes place on the wall of the left posterior cœlom opposite the aboral end of this ridge—and from this thickened patch a cord of cells grows into the ridge, gradually forcing its way in an oral direction; this is the characteristic core of the ovoid gland.

From this same thickening of peritoneum a cord of cells grows out in a direction parallel to the disc; this is the origin of the genital rachis.   By the outgrowth of a flap of peritoneum it is enclosed in a space which is called the aboral sinus.   The genital rachis and the space enclosing it both give off branches ·

one at each side of each arm. Local thickenings of these branches of the rachis constitute the genital organs. The surrounding spaces, the genital sinus (*ab gon*, figs. 122 and 123), is shut off from the aboral sinus by the outgrowth of a septum.

Fig. 99 is the marginal portion of a section vertical to the disc of a larva of Stage G. We see the rudiment of the ovoid gland (*ovg.*) as a fold projecting into the axial sinus. Further up we notice a thickened patch of peritoneum, which is invaginated into the septum separating the axial sinus from the left posterior cœlom (*pr. germ. inv.*). This is the rudiment from which, on the one hand, the genital rachis and, on the other, the core of the ovoid gland are derived. Figs. 100—103, similar sections to fig. 99, from a just metamorphosed star-fish, illustrate this. We see that from this rudiment a cord of primitive germ cells has grown out and filled the fold which is the rudiment of the ovoid gland. The last two sections cut a more oral portion of the fold, since they are slightly oblique; we see (figs. 102 and 103) that this core has not as yet penetrated to the oral end of the fold, and, further, that the fold is attached to the oral side of the inner perihæmal ring, or, in other words, that it traverses the lower end of the axial sinus, and is attached to its lower side. The original invagination to form the germ cells is situated at the very tip of the right dorsal horn of the left cœlom, where it meets the right ventral horn, but at this level the two horns do not open into each other (see p. 249). Figs. 104—106, again representing sections vertical to the margin of the disc, are taken from a young star-fish, in which R equals ·4 millimetre. Fig. 104 shows the cord of cells which arises from the peritoneal invagination and penetrates the dorsal organ, and the relation of this cord to the right hydrocœle and the axial sinus. We see that now this core of cells reaches to the oral end of the ovoid gland, and penetrates also a prolongation of the same, which is prolonged as a fold, hanging from the aboral wall of the inner perihæmal canal (figs. 105 and 106).

Pl. XVIII, fig. 110, which represents a similar section to figs. 99—106, shows practically the adult condition of the ovoid

gland and neighbouring organs. We see that the madreporic pore has commenced to be divided into two by the ingrowth of a fold. It is not the case in Asterina, as far as I can make out, that the numerous pore-canals found in the fully grown adult are derived from fresh perforations, as Cuénot has stated (3). Rather the statement which he quotes from Perrier seems to give the actual method of their formation.[1] We see that the openings of the stone-canal proper and the pore-canal into the axial sinus are still maintained. The ovoid gland with its core is seen to reach right down to the oral end of the axial sinus, and to be attached to its oral wall. Embedded in the septum dividing the inner perihæmal ring-canal (lower end of the axial sinus—see woodcut 1) from the perihæmal spaces proper is the so-called oral blood-ring (*sang. circ.*). This is a ring-shaped tract of peculiarly modified connective tissue; the section shows that it is of a different nature from the ovoid gland, and has no connection with it. In Asterias this ring gives off radial prolongations traversing the longitudinal septa of the radial perihæmal canals, but these do not exist in Asterina. The development of this structure as far as its histology is concerned is shown in Pl. XVII, figs. 107—109, which represent small portions of sections parallel to the disc. The first two sections are taken from the same specimen as figs. 82—84; in this specimen as we have already learned (see above, p. 248) the metamorphosis has just concluded. We see that the mesenchymatous tissue between the outer and the inner perihæmal rings has undergone differentiation. Most of it has become converted into fibrous tissue, but at one level no fibres have been formed, the whole of the mesenchyme cells becoming amœbocytes (*sang. circ.*); this part is the rudiment of the blood-ring. In fig. 109, taken from a specimen in which R equals ·45 millimetre, we see that the ring is completely formed;

[1] Durham, in a paper on "Wandering Cells in Echinoderms" ('Quart. Journ. Micr. Sci.,' vol. xxxiii), has described the communication of the axial sinus and stone-canal in a young Cribrella. He also insists that we have no blood-vessels, but rather "hæmal strands" in Echinoderms, but makes the common error of supposing the ovoid gland to belong to this category.

the intercellular jelly or plasma has acquired staining properties. To Leipoldt (9) is due the credit, in a careful paper on the anatomy of " the so-called excretory organ of the sea-urchin," of emphasising the fact that the ovoid gland and the oral blood-ring are of totally different nature; he describes branches from the blood-ring ramifying on the external surface of the ovoid gland.

The question arises, what is the true nature of this blood-ring? Cuénot (3) answers that it is a lymphatic gland, or centre for the formation of amœbocytes; and there is a great deal to be said for this view. We must, however, remember that structures of similar nature are found accompanying the alimentary canal in Echinids and Holothurids. Ludwig (13) has given a splendid description of their arrangement in the last group. He brings out with great clearness that they are tracts of connective tissue in which the fibres are sparse. The close relation of these " vessels " to the alimentary canal suggests forcibly that we may have here the first attempt at forming blood-vessels. There is certainly no propulsive organ or proper circulation, but the staining properties of the plasma show that it has been chemically altered, and the idea is suggested of some secretion from the gut-cells propelling itself along these tracts by the vis a tergo force of secretion. In the Asterid no close connection with the gut is observable,—the oral cœlom, in fact, intervenes between the œsophagus and the ring, as we have seen (p. 247); but the altered character of the plasma suggests that perhaps here some substance is formed necessary for the well-being of the organism, which then diffuses out into the neighbouring cœlomic spaces. The blood-spaces of the higher animals are known in many cases to be remnants of the blastocœle or segmentation cavity of the embryo; this has been shown in the case of Balanoglossus with great clearness by Spengel (21). Strictly speaking, therefore, the blood and lymph spaces of other forms are represented in Echinodermata by all the spaces in the body-wall unoccupied by fibrous tissue and dermal ossicles, and traversed by amœbocytes; but the blood-ring, gut vessels, &c., may be a first attempt at specialisation.

Figs. 113—117 are intended to illustrate the formation of
the genital rachis; and they all represent portions of sections
cut parallel to the disc; those portions, in fact, which are
transverse sections of one of the five interradial folds of the
body-wall which in the star-fish project into the body-cavity.
As we see in Pl. XVI, fig. 83, the axial sinus, right hydrocœle,
and the stone-canal, are embedded in one of these folds. It
follows that the cœlomic wall of this particular fold represents
the larval septum between the anterior cœlom and the pos-
terior cœloms; and its interradial position in the star-fish
becomes explained when we remember that the stalk with its
contained anterior cœlom lies opposite an interradius of the
water-vascular ring; which interradius is constituted by the
outgrowth of processes of the two lobes situated at the ends of
the hydrocœle, which is as yet an imperfect ring. These out-
growths meet, so to speak, above the neck of the stalk. Figs.
113 and 114 are from the same specimen as fig. 109. We
see the appearance of the rudiment of the germ cells in a
section parallel to the adult plane, and notice the remains
of the cavity of invagination (fig. 114, *pr. germ. inv.*).
Fig. 113 shows us that one horn of the right hydrocœle has
become embedded in the ovoid gland, and this is one reason
why it is extremely difficult to trace the continuity of the
primitive germ cells by sections taken parallel to the adult
plane, since the cord of cells is in some spots so narrow,
that it is therefore difficult to distinguish it from the epithelium
lining the right hydrocœle. Longitudinal sections, such as
fig. 104, show it much better. In figs. 115 and 116 (taken
from a specimen in which R equals ·7 millimetre) we see the
formation of the genital rachis; this takes place by a lateral
outgrowth from the primitive patch of invaginated peri-
toneum, from which we have seen the core of the ovoid
gland originating as an orally directed outgrowth; the aboral
sinus which surrounds it (*ab.*) is formed at the same time,
it is a portion of the cœlom shut off by the outgrowth
of a fold of peritoneum. Fig. 117, taken from a much
older specimen, shows the genital rachis in its complete form

in continuity with the original rudiment of the primitive germ cells.

It is, then, not quite correct to speak of the genital rachis as being an outgrowth from the ovoid gland, as Cuénot has done (3). This statement, nevertheless, marked a step in advance in our knowledge, for it gave a hint as to the meaning of the ovoid gland. Cuénot found specimens of Astropecten with the ovoid gland, but without the genital rachis, and noting the identity of the character of the cells in the two structures, stated that the rachis was an outgrowth from the gland, though he found no intermediate stages. These were first found by me (14) in the Ophiurid Amphiura squamata, and at the same time I demonstrated the epithelial origin of both gland and rachis. It is the genital rachis which of course was formerly known as the aboral blood-vessel; in most Asterids and Ophiurids it later undergoes partial degeneration, giving rise to cells containing violet pigment. Ludwig, however (11), and Hamann (7) have pointed out that the central core remains unaltered; the latter was the first to point out that in all Echinoderms, except Holothurids, a genital rachis exists, of which the genital organs are local outgrowths. In Amphiura squamata, however, and in Asterina gibbosa, according to Cuénot (3), the whole genital rachis remains unaltered through life; this is only one of the many points in which Asterina shows itself to be one of the most primitive of Asterids. In the plans given in text-books of the blood system, two vessels are shown proceeding from the aboral ring in the interradius of the madreporite to the pyloric sac. These are two mesenteric bridles, remnants of the piece of septum left at this level between the two horns (right dorsal and right ventral) of the left cœlom. At this spot the right (aboral) cœlom breaks through into the left (oral) cœlom, perforating the piece of tissue referred to, and leaving only the mesenteries. The peritoneum covering them seems to be peculiarly modified, and is possibly a place where the amœbocytes of the cœlomic fluid are formed.

The genital rachis gives off, as it passes each interradius, two branches enclosed in corresponding branches of the aboral

sinus (*gen. r.*, woodcut 1); one of these branches runs in an oral direction down each side of the interradial septum.   This septum is an ingrowth of the body-wall, which has by this time become marked, though its first beginnings date back to the end of the metamorphosis (Pl. XVI, fig. 84).

A section of one of these branches in an older specimen is given in Pl. XIX, fig. 119).   These genital branches are formed as the rachis reaches each interradial septum before it has formed a circle; in one specimen I have observed a rachis reaching only to the next interradius, and there giving off one genital branch.   Figs. 120 and 121 (taken from the same specimen as fig. 119) show the first rudiments of the genital organs.   The branch of the rachis ends in a swelling accompanied by a dilatation of the aboral sinus, and we see the beginning of a septum tending to shut off the main aboral sinus from this dilatation.   This septum was first described by Cuénot (3), and in it the genital duct is formed.   This is shown in fig. 123, taken from the oldest specimen I examined, in which R equals 8·7 millimetres.   We see that the genital duct is formed by a core of primitive germ cells burrowing its way through the body-wall.   Fig. 122, from the same specimen, shows the continuity of the rachis and the ovary.   We notice also the formation of follicles from the indifferent germ cells.

We are now in a position to compare the arrangement of the ovoid gland and genital rachis and their accompanying spaces in Amphiura squamata with that found in Asterina gibbosa.   In the former I described the genital rachis issuing from the oral end of the gland and accompanied by three spaces, which I named sinus *a*, sinus *b*, and sinus *c* (Pl. XVIII, fig. 112).   This figure is a diagram of a section parallel to the long axis of the stone-canal.   Fig. 111 is a diagram of a similar section of Asterina, but it is not quite accurate, since it shows both the ovoid gland and the stone-canal, and these two structures do not lie in the same radial plane in Asterina. In order to avoid obscuring the opening of the stone-canal into the axial sinus, it is necessary to indicate part of the ovoid gland by dotted lines.

Comparing figs. 111 and 112 we see that the axial sinus of Asterina is represented in Amphiura by sinus *c*, the so-called "ampulla." The aboral sinus (*ab*, fig. 111, sinus *a*, fig. 112) is also obviously homologous in both.

[Since my paper (14) was published, and since the present work was sent in for publication, I have made a careful re-examination of my sections of Amphiura squamata, and have arrived at a more complete comprehension of the structure and development of the ovoid gland and the neighbouring spaces in that animal. The space marked sinus *b'* (fig. 112) is not, as I formerly supposed, a part of sinus *b*, but is quite distinct. Sinus *b'* probably represents the right hydrocoele; it is already present in the youngest specimens I examined. Sinus *b** is a portion of the coelom shut off by the outgrowth of a flap of peritoneum; from the inner wall of this sinus the cells which at the same time give rise to the ovoid gland and to the genital rachis take their origin; it is obviously homologous to the cavity of the invagination of the primitive germ cells (*pr. germ inv.*, figs. 110 and 111), only in Asterina this space disappears.—December, 1895.]

We observe that the arrangement in Amphiura might be obtained from that in Asterina by rotating the stone-canal and accompanying structures outwards and downwards through an angle of 180°. That this is what has occurred in phylogeny is indicated, not only by the fact that in the young Amphiura the madreporite is near the edge of the disc and the stone-canal almost horizontal, whereas in the adult the madreporite is situated far in towards the mouth on the oral surface, but also by the curious undulating course of the genital rachis, which is aboral in the interradii and oral in the radii. This points to the conclusion that the aboral parts of the interradii

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* In my paper on this subject (14) sinus *b* is referred to as the axial sinus—it was formerly supposed to be continuous with sinus *c*, though Ludwig knew this was not so. At that time the meaning of the axial sinus in Asterids which Bury first suggested (2) was not generally known, and his interpretations were not accepted, and hence two different spaces were called axial sinus, one in Asterids and the other in Ophiurids.

have greatly developed, and have grown in between the radii on
to the oral surface, forcing the original oral plates to the extreme
centre of the disc; and so the stone-canal has been swung round
and the genital rachis pulled out of shape.   Now in Asterina
gibbosa there is a trace of this process; the rachis does
not, as Hamann (7) has described in Asterias, lie in one plane,
but pursues an undulating course, being much more aboral in
the radii than the interradii.   I am inclined to look upon this
as the primitive condition from which the Asterid and Ophiurid
arrangements have been derived.   I may as well mention here
some other facts which indicate the primitive nature of Asterina.
Chief among them is, that in the family of which it is a member
we meet with the most rudimentary form of those characteristic
Asterid organs the pedicellariæ.   We have in Asterina the
aboral surface covered with small spines, arranged in twos and
threes, and acting on irritation like pedicellariæ.   It is true
that some Asterids have no pedicellariæ, but here the evidence
from allied genera (cf. Luidia and Astropecten) suggests that
they have been lost; Asterina, however, shows us pedicellariæ
in statu nascendi.   The simple biserial tube-feet also con-
stitute a primitive character.

Fig. 118 represents ovoid gland and stone-canal in the
latest stage examined by me.   The gland is attached by an
exceedingly narrow pedicle to the wall of the axial sinus.
Its surface is thrown into deep folds, and the peritoneal
lining of the axial sinus, which forms its outer covering, is
modified, consisting of cylindrical cells with projecting rounded
ends. The interior of the gland is filled with a mass of primitive
germ cells supported by fibres, doubtless of mesenchymatous
origin.   I was unable to find any trace of a tube lined by
primitive germ cells, such as was discovered by Hamann in
the young Asterias.

What, we may finally ask, is the function of this strange
organ?   Cuénot, as usual, maintains that it is a lymphatic
organ.   This I am disposed to doubt very strongly; the
cells which it contains are of quite a different nature from
the amœbocytes of the oral blood-ring, and the evidence that

Cuénot brings to show that they escape by diapedesis into the axial sinus is quite insufficient. The cells of outer epithelial lining are not flattened but cylindrical, and I strongly suspect that he has mistaken their freely projecting ends for escaping amœbocytes; and I may remark that this curious outer epithelium shows its distinctive character from the time the first rudiment of the ovoid gland appears. Whatever its function may be now, there is no doubt that the ovoid gland was primitively a part of the genital organ, and probably is a remnant of the arrangement of the reproductive cells before the radial symmetry was acquired. It is interesting to notice that it originates from the left posterior cœlomic wall, whereas an analogous organ in Crinoids arises in the right or aboral cœlom, so that they are not strictly homologous.

If Hamann is, as there is strong reason to suppose, right in stating that the primitive germ cells wander along the rachis into the genital organ, it seems very probable that, at any rate in the young adult, the ovoid gland is a centre of formation of the primitive germ cells; and its relation to the axial sinus may have to do with its aëration, for it must be remembered that the pore-canal opens into the axial sinus, and the current in this is, as we shall see, inwards. In the fully grown adult it no doubt undergoes, to some extent, the degenerative change noted above in the genital rachis of other genera. What the meaning of this change is, is very obscure. Observations on the histology of the gland at different seasons might elucidate its meaning.

Turning now to the stone-canal, we see, in fig. 118 (a section transverse to the axial sinus and stone-canal), the beginning of that curious T-shaped ingrowth which is so marked a feature of the stone-canals of Asterids, but which is much less developed in Asterina than in other genera. It is covered by short cilia, the rest of the epithelium bearing long flagella.

Cuénot asserted that the stone-canal was a functionless rudiment, the current being neither outwards nor inwards. Ludwig[1]

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[1] Ludwig, "Ueber die Function der Madreporenplatte und des Steinkanals der Echinodermen," 'Zool. Anz.,' 1890, p. 377.

subsequently showed that in the stone-canal of Holothu-
rids and Echinids the direction of the current is inwards.
He examined the stone-canal cut out of the living animal; I
have confirmed his result by a somewhat more satisfactory
method.   I kept Amphiura squamata living for several days
in sea water, carrying in one case carmine, and in another
lamp-black in suspension; and on cutting sections I found
these particles in the pore-canal, and in some cases apparently
ingested by the cells lining it.   In view of Ludwig's researches
Cuénot comes in a later paper (4) to what I believe to be the
correct solution of the question of function.   He there suggests
that the flagella lining the stone-canal are always tending to
produce an inward current, and that thus the turgidity of the
whole water-vascular system is kept up.   [This is practically
the old view; except that he does not assert a continuous
inward current.—December, 1895.]

It is obvious from the structure of the valves of the tube-
feet that, in consequence of the ambulatory movements, there
must be a slow loss of fluid.   The ampulla and the tube-foot
are shut off from the canal leading into the radial water-vascu-
lar canal by a pair of valves opening only inwards.   Conse-
quently during the contraction of either ampulla or tube-foot
the two act together as a closed system, since no fluid can escape
into the radial canal.   The existence of the valves however shows
clearly that fluid occasionally enters the tube-foot, and this can
only be rendered possible by a slow loss of turgidity owing to
the osmosis of the contained fluid when under pressure.   This
is confirmed by considering the case of Ophiurids, where (except
in the Astrophytidæ), the tube-feet having lost their ambulatory
function, the madreporite has only one or at most two pores,
and the calibre of the stone-canal is exceedingly narrow.

The dermal branchiæ arise when the star-fish has reached a
diameter of about 1·5 millimetres (R equal ·85 millimetre).
We see that the branchia is only a very thin piece of the body-
wall produced into a finger-like process (Pl. XVI, fig. 98).
Around the base of the branchia is a peribranchial space lined
by flattened epithelium: this space, as Cuénot has rightly

observed, is the only one of the great "schizocœlic" spaces which Hamann (8) has described in the body-wall which has any real existence, the others being merely artefacts produced by the process of decalcification. I have found one specimen showing the first trace of a dermal branchia (figs. 96 and 97). We see a slight thickening of the peritoneum, and above it the peribranchial space. Fig. 96 shows that the latter is a diverticulum of the cœlom. As I have only one section illustrating this I do not speak with absolute certainty on the point; but, with this possible though very improbable exception, there is no schizocœle whatsoever in Asterina gibbosa: all spaces lined by epithelium are of cœlomic origin.

Histological Differentiation.

The cells of the gut-wall have undergone some change since the close of the metamorphosis. Specimens of the epithelium from different regions are given in Pl. XIX, figs. 129—132. These are all taken from a young adult in which R equals ·85 millimetre. The cells of the lateral walls of the stomach (i. e. the adult œsophagus) have become exceedingly long and narrow; their outer ends are refracting and take a light yellow tone with osmic acid (fig. 129). The cells of the aboral wall, on the contrary, have developed numerous gland cells filled with globules; interspersed amongst them are some very narrow filamentous cells. Fig. 130 shows the spot marked × where the stomach opens into the pyloric sac and the abrupt change in the character of the epithelium. The pyloric sac is lined by uniform columnar cells; the nucleus is generally near the base of the cell, and is never placed further up than the middle, and the protoplasm is uniformly granular (fig. 131). The cells lining the rectal cæcum (fig. 132) are similar in form but smaller, and the protoplasm is clearer, with the outer part more refringent. It is at least a plausible suggestion that the gland cells of the stomach secrete the poison which paralyses the prey, and that the cells of the pyloric sac give rise to a digestive ferment.

The differentiation of tissues which has gone on in the

body-wall is illustrated in Pl. XXI, figs. 146 and 147. These sections are taken from young adults in which R equals ·4 mm. and ·86 mm. respectively, and they pass through the same region as fig. 145, which is from a larva in Stage E, and which we have already described. In fig. 146 we see that the muscular fibres of the muscle we may call the dilator ani are still connected with the peritoneal cells; but in fig. 147 they have become quite distinct, and the cells of the peritoneum have become quite flattened. The ectoderm has entirely changed its character, the numerous larval goblet cells have almost disappeared, and the cells in general have become shorter; many of them are inversely wedge-shaped, and are apparently about to become converted into gland cells, probably of the same histological character as those of the aboral wall of the stomach. Here and there is a narrow cell ending in a fine hair, one of the scattered sense-cells of the aboral surface; these are shown in fig. 148, a piece of ectoderm from another individual of the same age. All observers agree in maintaining that the ectoderm of the adult retains its ciliated covering; but though I have been able to make out easily the cilia, or rather flagella of the metamorphosing larva, I have not been able to do so with any certainty in the aboral wall of these young adults. Probably the cilia are very delicate and fragile. The tissues of the mesenchyme have undergone marked differentiation. So far as my researches have extended it seems that three fates are open to mesenchyme cells, all of which are illustrated in fig. 147. They may remain practically unchanged as amœbocytes or wandering cells (*amœb.*), or they may become embedded in bundles of fibres so as to form connective-tissue cells (the fibres being intercellular, not outgrowths of cells); or, finally, they may fuse to form a syncytium having the form of a meshwork (*calc.*). This is the skeletogenous tissue; lime is deposited in the interstices of the meshwork. There is a fourth fate, which is not reached by any as far as I have gone, but which obviously must be the lot of some, and that is to form the muscles moving the spines or rudimentary pedicellariæ. The superficial position of these muscles renders it exceedingly

unlikely that they are of peritoneal origin, and their position in other Asterids where, as in Asterias, for example, they occur on the skin covering the spines, growing even from their tips, makes such a supposition almost impossible. Therefore we must postulate some muscles of mesenchymatous origin for Asterina, although all those which I have examined are of epithelial origin.

The development of the nervous system has advanced greatly, and has reached, as soon as the metamorphosis is complete, its final form; this is shown in fig. 141, taken from the same specimen as fig. 146. The ectoderm cells have increased immensely in number, and become excessively filamentous, so that the nuclei are many layers deep; the fibrillar layer has increased very much in thickness. It is traversed by vertical fibres which sometimes branch and sometimes have small nuclei on them; these are in continuity with the ectoderm cells, but are probably of non-nervous character. Sections parallel to the disc show that numerous little bipolar cells are embedded in the mass of fibrils (Pl. XVII, fig. 109, *bip. gang.*). Since these cells are not present in the just metamorphosed form, they must be ectoderm cells which have passed in, and occasionally one sees a cell just at the boundary of the fibres apparently in the act of passing in. The perihæmal spaces become closely apposed to the nerve-cord, no mesenchyme being left between (*ph.* fig. 141); the vertical fibres do not, however, arise in connection with the epithelium of these cavities, since they are present before this close apposition takes place. Cuénot states that all the ectoderm cells of the nerve-cord end in the vertical supporting fibres described above. This is a bold statement which it is quite impossible to prove by sections, and which is most improbable. As a matter of fact these vertical fibres are not present in nearly large enough number to account for all the ectoderm cells; and Hamann's statement (8) is probably correct, that many of these end in fine processes which lose themselves in the mass of fibrils.

The sense-organs of Asterina are all developed in connection with the appendages of the water-vascular system. The eye

arises at the base of the terminal tentacle of the radial canal;
two stages in its development are given in Pl. XXI, figs. 142
and 143.   In the first we see a simple ectodermic involution; in
the second we see a pit surrounded by columnar cells, pro-
bably retinal, and filled up by closely fitting polygonal cells,
which correspond to the layer of vitelligenous cells in an
Arthropod eye.   The existence of these cells has been vigor-
ously denied by Cuénot (3), who maintains that we have only
polygonal cuticular plates.   My sections, however, remove all
doubt on the subject; they show with perfect clearness that we
have to do with cells, and their nuclei can be made out.   This
pit is the first only of the numerous pits which cover the " eye "
of the adult, which is really essentially a small rounded
swelling at the very tip of the radial nerve.   The method
of preservation employed seems to have dissolved the pigment.

The remaining sense-organs are the tips of the
tube-feet and the terminal tentacle.   A longitudinal
section of a tube-foot is given in Pl. XXI, fig. 150.   This is
taken from a specimen in which R equals ·4 millimetre, but
it holds true for specimens of a radius of a millimetre or more,—
that is, for probably the first two months after the metamor-
phosis.   Comparing it with fig. 149, a similar section taken
from a larva in Stage F, we see that the ectoderm at the tip
has become thickened, and underneath it we can make out on
each side a mass of nerve-fibrils.   A powerful nerve leaves the
radial nerve-cord to supply each sense disc; it would be more
correct to speak of these branches as actual prolongations of
the nerve-cord with its cells and fibrils; they are, indeed, the
only conspicuous branches which it gives off.   Some of the
ectoderm cells of the sense disc have a peculiar regular cylin-
drical form, which recalls that of the retinal cells.

The facts above related justify the view that the whole radial
canal with its tube-feet is to be looked on as one large branched
tentacle, the main function of which was probably originally
prehensile and therefore also sensory; and since a plexus of
nerve-fibrils is in the adult found under the ectoderm all over
the body, the central nervous system may be said to be a local

concentration of this in the neighbourhood of a greatly deve-
loped sensory tentacle. The support of this tentacle by the
arm is a secondary matter, as we have already learned—a fact
which comes out still more clearly in Crinoid development.
There the primary hydrocœle lobes develop into long free
tentacles covered with sensory hairs. At a very late period
(later than any which Seeliger observed) these primary tentacles,
according to Perrier (17) become applied to five outgrowths
of the body-wall; these latter immediately bifurcate to form
the ten arms, and so the free tips of the tentacles are situated
each in the angle between a pair of arms. Seeliger (18) adduces
this last fact to show that the primary tentacles are not the
same as the primary hydrocœle lobes of Asterids, forgetting
that the point where a pair of arms diverge corresponds to the
tip of the Asterid arm, since in Antedon there are ten arms
which have arisen by dichotomy from five.

The epithelium of the water-vascular system in fig. 150
shows an interesting feature; the cells have developed muscular
tails which are arranged longitudinally, and the important point
is that these myo-epithelial cells persist as such for a
considerable period of free life.

Pl. XXII, figs. 151—154, show us that the aboral wall of the
perihæmal space also gives rise to muscles. These connect
one ambulacral ossicle with its fellow of the opposite side, and
serve, by approximating these to one another, to close the ambu-
lacral groove. Figs. 151 and 152 show us that here again we
have, in the first instance, to do with myo-epithelial cells.
Muscles connecting one ossicle with its successor and prede-
cessor are also present, but very much more feebly developed.
In Ophiurids, however, as is well known, they are most power-
ful, and this point gives the key to nearly all the peculiarities
of this group as compared with Asterids. Presuming, as we
fairly may, that these muscles are developed from the peri-
hæmal wall as in Asterids, we are brought face to face with a
most interesting effect which this produces on the nervous
system. Fig. 156 gives a section of the radial nerve-cord of an
Ophiurid. We notice two great masses of cells and fibres on

the aboral side of the nerve-cord, and Hamann (8) has shown that the nerves for the ambulacral muscles arise entirely from these.

Now it has been for a long time suspected, and Cuénot has finally proved it (4), that there is a similar but feebler development of what we may call "cœlomic nervous tissue" takes place in the Asterid. None of my specimens were old enough to show this, though one can see (fig. 141) that the perihæmal epithelium has come into intimate connection with the nervous matter. Pl. XXII, fig. 155, represents a transverse section of the nerve-cord of a young Asterias; we see in it that this epithelium has become thickened on each side of the median septum; one requires, however, a section of the nerve of a fully grown adult to see the cœlomic nervous fibrils. So we may say that from their aboral wall the perihæmal spaces give rise to muscles, and from their oral wall to the corresponding nervous tissue. I ought to mention in this place that Cuénot describes a canal leading from the perihæmal space into the cœlom at the level of each ambulacral ossicle; also five pores leading from the outer perihæmal ring to the cœlom. If these communications exist, they are certainly secondary, as there is no trace of them in my specimens; but as Cuénot's results were founded on injection I am exceedingly sceptical as to the existence of such openings.

I have said above that the increasing importance of the ambulacral muscles is the explanation of the evolution of Ophiurids from Asterids. The Ophiurids have substituted the quick powerful movements of these muscles for the slow motions of the tube-feet. In correlation with this change the nervous system has become better developed, the radial cords becoming gangliated, and the whole is removed from the exterior by invagination, and thus the subneural space is really a neural canal. The ambulacral ossicles have become firmly united, each to its fellow, to form a series of vertebræ, and thus the cavity of the arm is reduced, and this, with the simpler food, accounts for the disappearance of the pyloric cæca.

We have already pointed out that the lessened activity of

the tube-feet, consequent upon the loss of the locomotor function, explains the reduced stone-canal and madreporite, though probably their increased sensitiveness has helped in developing the nervous system.

Literature consulted.

An account of the earliest publications on Echinoderm development is not given here, since a résumé of them will be found in the papers I quote; and I hold it to be a waste of time to reiterate with each new paper the whole history of the growth of our knowledge ab initio. I mention here only those authors on whose results I have, so to speak, built, or from whom I have found it necessary to differ. Ludwig's work on the anatomy of Asterids (10) laid the foundation of our knowledge of the hæmal and perihæmal systems; though, as we have seen, many of his ideas about these structures were incorrect. Subsequently in treating of Ophiurids (11) he discovered the genital rachis. Hamann (7) extended this result, and pointed out the amœboid nature of the primitive germ cells. Then we had Ludwig's great work on the development of Asterina gibbosa (12), the first account of the metamorphosis of any Echinoderm which had any pretence of completeness, and to which I have constant occasion to refer. His account of the changes in external form and of the development of the calcareous plates can hardly be improved upon. Owing, however, to the imperfect methods in vogue at that time he failed to penetrate with equal success into the course of the internal changes. He saw nothing of the segmentation of the cœlom or of the ring-like growth of the left cœlomic vesicle; he saw nothing also of the origin of genital organs, ovoid gland, or oral cœlom. He did not observe the right hydrocœle or find the origin of the perihæmal spaces. He missed the fixed stage, and he does not seem to have had any clear conception of the relation to each other of the larval and adult planes of symmetry. We owe to him, however, the clear distinction of pore-canal and stone-canal, and the recognition of the fact that the pore-canal is completely independent of the

hydrocœle.   Bury (1) may be said to have introduced modern
conceptions of Echinoderm development by his work on the
development of Antedon; there he distinguished between an-
terior cœlom and hydrocœle, and showed that the stalk was the
præoral lobe.   Then he made a series of observations on Echino-
derm larvæ (2), and showed that generally speaking the cœlom
on each side becomes segmented into two vesicles, an anterior
and a posterior.   He, however, regarded the hydrocœle as an
essentially unpaired structure, an outgrowth from the anterior
cœlom, and was greatly distressed to find that it originated
from the posterior vesicle in Ophiurids, and that in Asterina
the stone-canal, which in other forms represented the original
neck of communication between anterior cœlom and hydrocœle,
was apparently an independent perforation.   The last difficulty
has been answered by Ludwig;[1] as to the former, the proof I
have brought that the hydrocœle is paired shows that there are
really three primary divisions of the cœlom on each side, viz.
the anterior cœlom, single in Asterina, but primitively paired
in Asterias; the right or left hydrocœle, and the posterior
cœlom (right or left as the case may be); the apparent forma-
tion therefore of the hydrocœle from the anterior or posterior
vesicle is a mere question as to whether the septum between
the posterior cœlom and the hydrocœle or the septum between
the hydrocœle and the anterior cœlom is formed first.

In speaking of the Bipinnaria, Bury says that in a future
paper he intends to prove that the anterior cœlom becomes the
axial sinus, but up till now he has published nothing further
on the subject.[2]   He made a few observations on Asterina

[1] Bury had not seen the stage of development when the stone-canal is an
open groove.

[2] Since the preliminary account (15) of the present paper was published, a
paper on the "Organogeny of Stellerids," by M. Achille Russo, has appeared
in the 'Atti della Accadema reale di Napoli' for 1894.   In this work (to
which I only obtained access some considerable time after the present paper
was finished) M. Russo gives a description of the ontogeny and anatomy of
the ovoid gland and axial sinus in Asterina gibbosa and an Ophiurid.   He
combats my statements about the origin of these structures in Amphiura
squamata.   The origin of the axial sinus in Asterina has been correctly de-
scribed; it is about the only thing that is correctly described in the paper.

larvæ of Stage D, and saw the completely closed cœlomic vesicle on the right, and the imperfect transverse septum on the left side, and was at a loss how to interpret these appearances; the right hydrocœle he calls a mesenchymatous vesicle.

It is curious to see how unable many zoologists have been to grasp Bury's idea of the anterior cœlom; thus Seeliger, who has confirmed his work on Antedon and amplified it till it may be said that we have an exhaustive knowledge of the subject, objects to consider the structure Bury named anterior cœlom as such, on the supposition that Bury meant by that a fellow of the hydrocœle, which it obviously is not. Seeliger calls it the "parietal canal," but the structural facts he so accurately relates are convincingly in favour of Bury's interpretation. The weak point in Bury's observations on Plutei and other larvæ was that in no case were any more than a few stages taken at random examined; but I hope the account I have given in this paper will provide a more solid basis for the idea of segmentation of the cœlom in Echinoderms. Field (5) has published a short paper on the development of the Bipinnaria; he carries it up only to a stage corresponding to midway between Stages B and C of Asterina. The chief points of interest in the paper are that many of the larvæ had two madreporic pores, and he suggests that this is a normal stage in the ontogeny; also that the two ciliated rings characteristic of the Bipinnaria are derived from one, and that there is a præoral sense-organ comparable to that in Antedon.

This paper does not contain the discovery that the watervascular rudiment is paired; for, as a matter of fact, in the oldest larva examined no trace of the left hydrocœle was present. The "schizocœlic space," near the madreporic pore, may represent the rudiment of the right hydrocœle; needless to say, it was not recognised as such.

Theel (22) has recently succeeded in following the metamorphosis in Echinocyamus pusillus so far as the external features are concerned. He finds that already in the blastula

M. Russo's technique was obviously not equal to dealing successfully with such difficult subjects as Echinoderm larvæ.

a præoral sense-organ is present; this subsequently becomes incorporated with the ciliated ring, and if this organ is homologous with that of the Bipinnaria, we may conclude that the ciliated band of the Pluteus corresponds only to the posterior of the two bands of the Bipinnaria, since in the Bipinnaria the sense-organ is situated between præoral and post-oral ciliated bands, and this spot corresponds to a constriction in the original longitudinal ciliated ring, not to a position on its anterior edge.

Our knowledge of Echinoderm histology is largely due to Hamann (8) and Cuénot (3 and 4). The latter, as we have seen above, was the first to suggest that the ovoid gland gave rise to the genital rachis. The first account of the development of ovoid gland and rachis is given in my paper on Amphiura squamata (14), and I have there collected the fragmentary notices on this subject, which had till then appeared.

[I regret that when I sent in this paper for publication I did not mention the well-known paper of Metschnikoff (" Studien über die Eqtwickelung der Echinodermen und Nemertinen," ' Mémoires de l'Académie Impériale de St. Pétersbourg,' tome xiv, No. 8), in which he describes a right hydrocœle in Amphiuria squamata. He there says that the right cœlomic vesicle becomes divided into anterior and posterior portions just like the left; the anterior portion sometimes atrophies but sometimes develops into a regular five-lobed hydrocœle. It has been the fashion to ignore this work, since it was not accomplished by modern methods; but after my experience with Asterina I feel morally certain that Metschnikoff was right, though of course he did not distinguish between hydrocœles and anterior cœlom. Bury (2) seems to have missed the importance of this observation.—Dec., 1895.]

General Considerations.

On reviewing the developmental history recorded in this paper, two main questions present themselves: first, what light does it throw on the affinities of the Asterids with other Echinoderms? and second, does it suggest any direction in

which we may look to find the origin of the group Echino-
dermata as a whole?

In answer to the first question, we must observe that the
stalks of Asterina and Antedon are morphológically equivalent,[1]
both being formed from the præoral lobe, and, so far as one
might judge from the different shape of the latter in the two
cases, the adhesive discs by which they fix themselves are
situated in precisely the same position. Now no one doubts
that Antedon had a fixed ancestor; it is, in fact, one of the
very few Crinoids which do not remain fixed throughout their
whole life. If Asterids ever had an ancestor in common with
Crinoids which could be called an Echinoderm at all, it must
have been one represented by the fixed larva of Antedon before
it has fully acquired radial symmetry, since, as we have already
pointed out, the metamorphoses of Antedon and Asterina
pursue different courses. In the first case the mouth is shifted
backwards and upwards, and a precisely similar thing happens
to the larvæ of Entoproct Polyzoa, Ascidians, and Cirri-
pedes when they fix themselves. In the second case, how-
ever, the disc is flexed obliquely downwards on the stalk, so that
the left cœlomic sac and the hydrocœle both come to encircle
the base of the stalk; and as consequence the aboral poles in
the two cases are not homologous, for in the first case this pole
is the cicatrice left by the rupture of the stalk, whereas in the
second case the point where the stalk passes into the disc is
quite remote from the aboral pole. The apparent correspondence
of the calcareous plates of the calyx in Antedon and the so-
called calyx in Asterina is simply due, in my opinion, to the

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[1] Since the present paper was sent in for publication, my attention has been
called to some observations of Perrier's which I regret having overlooked. In
his account óf the Echinoderms collected by the "Mission Scientifique du Cap
Horn," he describes the larvæ of Asterias spirabilis, which adhere to the
buccal membrane of the mother. They are attaćhed by a pedicle which
Perrier compares to the stalk of the Antedon larva and to the præoral lobe of
the Asterina larva. He points out that both in the case of Asterias spira-
bilis and of Asterina gibbosa the pedicle arises from the oral surface, whereas
in Antedon it is aboral in its origin, but he offers no explanation of this dif-
ference in position.

fact that their arrangement is in both cases dominated by the prevailing pentamerous symmetry of the adult.

The reason why the change in the position of the mouth takes place in Antedon is that this animal, like the others in which a similar change occurs, feeds on swimming or floating prey, and, so to speak, turns the mouth upwards to receive it. Asterids and their allies, on the other hand, find their food on the substratum, and therefore we must suppose that in the fixed ancestor of Asterids the body was flexed downwards so as to bring the substratum within reach of the tentacles.   The difficulty suggests itself that a fixed form finding its food on the substratum might very soon devour all within its reach ; and the suggestion may be made that perhaps the ancestor of Asterids never was fixed, but that the divergence from Crinoids took place when the common ancestor was a creeping form, since we may reasonably conclude that creeping habits formed the transition stage between a free-swimming and a fixed mode of life.   In this case, however, the difficulty meets us of accounting for that radial symmetry which is so deeply impressed on the organisation of Asterids and other forms.   It would be rash to say that fixed life is the direct cause of radial symmetry when we consider the case of Brachiopods, Cirripedes, &c., but this symmetry is only, so far as our knowledge goes, developed in connection with a fixed life.[1]

The proximate cause of the radial symmetry of Asterids is the immense preponderance of the organs of the left side, and it is difficult to see how this could have gone on to the extent it has done in an animal which moved about with a definite part directed forwards.   The motion of the Asterid when metamorphosed is vague,—that is, any part is directed forwards; and it seems to me that a fixed stage must intervene between this and the mode of motion in which the head went first.

[1] Some might object that Ctenophores and Medusæ are radially symmetrical, but the first are not truly so; and as to the second, I hold very strongly the view that the Medusa is only a specialised bud, which has secondarily acquired locomotive powers in order to disperse the ova. Its radial symmetry has been inherited from fixed ancestors.

Therefore I feel that we are shut up to the supposition that Asterids had a fixed ancestor, and we must suppose that this form lived under conditions where enough food drifted along the bottom to meet its demands. Pl. XXII, fig. 157, represents the characters which I consider the common ancestor of all Echinoderms possessed when it became fixed. Figs. 158 and 159 show how these characters became modified in the cases of the Asterid and Crinoid respectively.

It is probable that a fixed stage occurs in the life history of all Asterids. The larvæ of Echinaster and Asterias Mülleri, which are carried in brood-pouches, certainly possess one, and the three papillæ on the Brachiolaria larvæ are generally interpreted as an apparatus for fixation.

The fixed stage has, however, been lost so far as we know in all other Echinoderms; and it is instructive to note in this connection that Asterids alone retain the great præoral lobe. This has completely atrophied in the Plutei both of Ophiurids and Echinids; and in the latter case, as I have indicated above, (page 273) there is some evidence to show that a præoral ciliated band has likewise disappeared. The Auricularia still retains a trace of the præoral lobe, and it has been regarded as an exceedingly primitive form because it retains the undivided longitudinal ciliated band, and because the larval mouth becomes the adult one. The internal anatomy of this larva shows that, except in these two points, it is the most modified of all; the anterior cœlom so conspicuous in the Bipinnaria is represented, as Bury has shown (2), by a bud of cells which forms the secondary madreporite on the stone-canal, and the whole mode of segmentation of the cœlom is most erratic.

I have dwelt on this subject at some length because some have regarded the Holothurids as the primitive group of the Echinoderms, and Sémon (19) has even attempted to show that the primary hydrocœle lobes in them became the oral tentacles, whilst the so-called radial canals were really interradial outgrowths. Ludwig (13) has, however, shown the incorrectness of this; in the Synaptidæ alone do the oral tentacles spring direct from the ring-canal, and it was the development of

Synapta on which Sémon based his theory. In all other Holo-
thurids the buccal tentacles spring like the buccal tube-feet of
Echinids from the proximal portion of the radial canals. It is,
however, difficult for me to see how anyone can doubt that the
Asterids are the least modified group of the Echinoderms. I
have already dealt with their relations to Ophiurids, and have also
pointed out that the Asterid central nervous system is really a
concentration of the diffuse nervous plexus in connection with
what must be regarded as a great sensory tentacle,—that, in fact,
the whole radial water-vascular canal is to be regarded as a
pinnately branched tentacle for which the arm is a secondary
support. Sémon himself has suggested this (20), and it comes
out even more clearly in Crinoid development than in the case
of Asterids. Now the long radial canals in Echinids, ending
in degenerate sense tentacles, clearly at one time had arms to
support them ; but these supports have been drawn back into
the body. The Holothurids have been probably derived from
the primitive Echinids ; their calcareous nodules are most
likely plates and spines atrophied in order to allow of free
muscular movement. The terminal sense tentacles of the
radial canals have entirely disappeared, and the forward shift
of the madreporite and genital opening is no more difficult
to understand than the varying position of the anus in Echi-
nids. In the Asterids alone is locomotion entirely dependent
on the tube-feet, and in them only we have the nervous system
exposed.

On the second question, viz. that of the affinities of the
Echinodermata as a whole, much light is thrown by the
development of Asterina gibbosa. It is of course well
known that the Tornaria larva of Balanoglossus shows a strong
resemblance to the Bipinnaria in the course of its ciliated
bands, and in possessing a præoral cœlom opening by a pore on
the left. The adult Balanoglossus has five cœlomic cavities,
and Bateson has shown that these arise as separate pouches of
the gut. The question arises whether it is legitimate to
homologise with these the five cœlomic cavities of the Asterina
larva which arise by division of pouches already formed, but

which still persist in the adult as sharply separated cavities, only the most posterior pair, viz. the right and left posterior cœloms (oral and aboral) of the adult having partially fused with each other.   The development of Antedon seems to answer this question in the affirmative.   In its case the hydrocœle is budded off quite independently of the posterior cœlomic sacs.

Adopting, then, the view that the cœlomic sacs of the Enteropneusta and Asterids correspond, we find that the hydrocœle represents the collar cavity.   Now in Cephalodiscus the collar cavities are produced into long pinnately branched tentacles, comparable to the radial water-vascular canals, and further a branch from the central nervous system accompanies each tentacle, just as the radial nerves accompany the radial canals in Echinoderms.   Now, if we suppose that the two hydrocœles of Asterina were equally developed and approximated in the mid-dorsal line, the fusion of the anterior portion of the two nerve "rings," which of course would in this case be only open curves (since a ring-form is attained through the preponderating growth of one side) would give rise to a mid-dorsal nervous system like that of Cephalodiscus.   Nor is that all; Professor Spengel (21) has shown in his monograph of the Enteropneusta that the currents in the proboscis-pore and collar-pore are inwards, and that by this means the animal inflates the proboscis and collar so as to render them efficient locomotor organs. We have seen that the function of the stone-canal is a similar one.

We conclude, then, that the free-swimming ancêstor of Echinoderms, for which we may adopt the name Dipleurula, and the Tornaria ancestor of Balanoglossus, were closely allied. This involves the assumption that they were allied to the Protochordata, for, as I have elsewhere stated (16), Professor Spengel's attempt to refute the Chordate affinities of Balanoglossus has been, in my opinion, futile.   Although it may seem somewhat fanciful, I cannot help seeing hints of Vertebrate peculiarities in the anatomy of Echinoderms.   Where else among all animals of higher grade than the Cœlenterates do we find calcareous ossicles in the dermis?   Where else

is the removal of the nervous system from the surface effected by invagination leading to the formation of a neural canal?

When we come to try and picture the characters which the Dipleurula possessed, we see at once that it must have been far more primitive than any existing form. In point of fact an Asterid is about the most undifferentiated animal above the level of Cœlenterates which exists. No proper blood-vessels, no specialised excretory organ, a central nervous system which is really a local concentration of a diffuse skin plexus, perfectly simple generative ducts, a most feebly developed muscular system, the fibres being for a considerable time simply myo-epithelial cells,—where is such a state of things to be found outside the Cœlenterata? When we further add that in the Crinoid the ambulacral nervous system nearly atrophies in the adult, and is replaced by a new system developed in a totally different position, we see that we are at about as low a level as one could well imagine, since the central nervous system in all higher forms is a most persistent structure.

Assuredly Platyhelminths, which have been usually regarded as the basal group in the Cœlomata, or better, Triploblastica, are far more highly specialised. To say nothing of their cephalic ganglia, we have their highly developed muscular wall and their complicated excretory and genital organs to prove this.

We shall not, then, go far astray in assigning the Dipleurula and the Tornaria to a group, the Protocœlomata, which were not far removed from the Cœlenterates; the cœlom was divided into three parts on each side, but of these the most anterior were usually fused to form an unpaired vesicle. The Dipleurula differed from the Tornaria chiefly in possession of an aperture, the stone-canal, in the wall separating the proboscis cœlom from the collar cœlom. This may have been the primitive arrangement, or it may have been a secondary arrangement acquired in consequence of the Dipleurula having lost the collar-pores, one of which may, however, as we have seen, be developed as a variation in the Asterid larva. At the apex of the præoral lobe was a more or less developed sense-organ with associated

nervous tissue. The collar cavities were probably prolonged into tentacles with which nervous tissue was associated.

If this supposition is correct, the group Protocœlomata was a pelagic cosmopolitan one, and it is in accordance with what we know of wide ranging groups that some of its members should adopt changed habits and modified structure. The Echinodermata, then, represent the earliest offshoot which took to a sessile life and acquired radial symmetry. A little later the Hemichordata branched off, a burrowing life being adopted and consequent degeneracy resulting. The main stem, however, remained pelagic and gave rise to the Chordata. The Ascidians were the next offshoot, and then came Amphioxus. We see, therefore, that the track of the great Chordata phylum through past ages is traced by examining those of its members who at very different periods of its history, and at different stages in its evolution, have forsaken their high vocation, and taken to a sessile or burrowing life, with the inevitable consequence—degeneracy.

The following diagram may represent these relationships a little more clearly :

Protocœlomata

Dipleurula

Hemichordata (Tornaria).
———————— Balanoglossus, Cephalodiscus.

Fixed ancestor of Echinoderms.

Crinoids.   Protochordata.

Asterids.   Ascidians.

Protoechinids.   Ophiurids.   Amphioxus.

Echinids.   Holothurids.   Vertebrata.
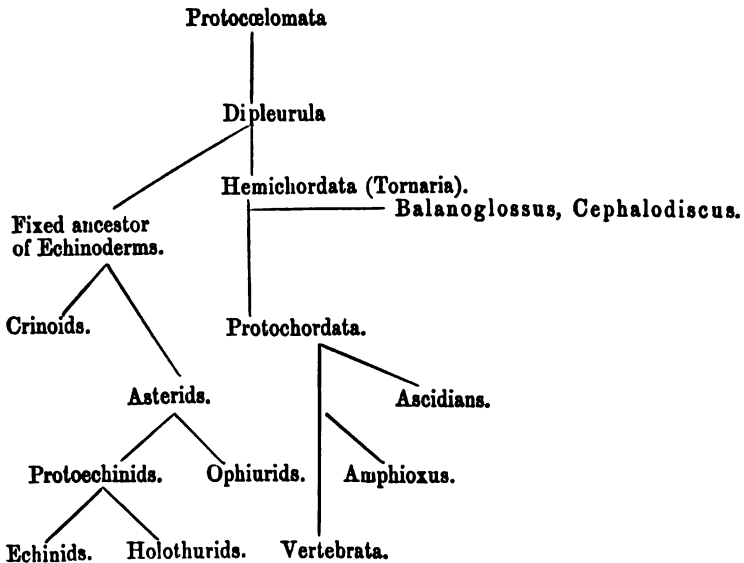
I hope in a future paper to be able to show that the Trochophore larva is also related, though much more distantly, to the Dipleurula.

<div style="text-align:right">Zoological Laboratory,</div>

March 8th, 1895.   Cambridge.

[POSTSCRIPT.—With reference to the point discussed on p. 275, viz. the existence of a fixed Echinoderm in which the tentacles were directed towards the substratum, it is of interest to note that in the fossil Crinoid Cheirocrinus the calyx was sharply bent on the stalk, so that the arms were directed downwards towards the substratum.]

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EXPLANATION OF PLATES XI—XXII,

Illustrating Mr. E. W. MacBride's paper on "The Develop-
ment of Asterina gibbosa."

(The outlines of all the sections figured were drawn with the camera lucida.)

List of Abbreviations used.

a. Anterior body-cavity and the part of it persisting in the stalk. *a'.* Axial
sinus. *ab.* Aboral sinus. *ab. gon.* Dilatation of branch of aboral sinus round
the gonad. *amb.* Ambulacral ossicle. *amœb.* Amœbocytes. *a. œ.* Adult
œsophagus or "stomach." *B.* Basal plate. *bip. gang.* Bipolar ganglion-
cells. *branch.* Dermal branchia. *C.* Centro-dorsal plate. *calc.* Calcigenous
tissue. *ect.* Ectoderm. *end.* Endoderm. *fibr.* Fibrous tissue. *fix.* Disc

on præoral lobe for attachment of larva. *gen.r.* Genital rachis. *gob.* Goblet cells. *hist.* Involution of ectoderm to facilitate histolysis. *lhy.* Left water-vascular rudiment or hydrocœle; its lobes are numbered with Arabic numerals. Roman numerals I, II, III, IV, V, denote the arm rudiments. *lo.* larval organ. *læ.* larval œsophagus. *lpc.* Left posterior cœlom. *l'p'c'.* The right ventral horn of the same. *l''p''c''.* The right dorsal horn of the same. *l.stom.* Larval stomach. *mes.* Mesenchyme. *mp.* Madreporic pore. *musc.* Muscular tissue. *musc.amb.* Ambulacral muscles. *musc.larv.* Larval muscles. *musc. retr.* Retractor muscles of adult œsophagus or stomach. *nerv.* Nervous tissue. *nerv. circ.* The nerve-ring. *nerv. larv.* Larval nervous tissue. *or. c.* Oral cœlom. *pbr.* Peribranchial space. *p. c.* Pore-canal. *p'c'.* Additional pore-canal in abnormal larva. *per.* Peritoneum. *ph.* Perihæmal space. The perihæmal rudiments are numbered 1.2, 2.3, 3.4, 4.5, and 5.1, according as they originate between the hydrocœle lobes 1 and 2, 2 and 3, 3 and 4, 4 and 5, and 5 and 1 respectively. *pr.germ.* Primitive germ cells. *pr.germ. inv.* Involution of the peritoneum whence these cells arise. *py.* Pyloric sac and its cæca. *ret.* Retinal cells. *rhy.* Right hydrocœle. Its lobes when they exist are numbered like those of the left hydrocœle, &c. *r'hy'.* Extra right hydrocœle present in abnormal larva. *rpc.* Right posterior cœlom. *sang. circ.* Oral blood-ring. *stc.* Stone-canal. *st'c'.* Extra stone-canal present in abnormal larva. *T.* Terminal plate. *tr.* Trabecula. *vit.* Cells forming crystalline body (Glaskörper). *wv.* Radial water-vascular canal. *wvr.* Water-vascular ring-canal.

PLATE XI.

All the figures are reproduced, though in a somewhat simplified form, from Ludwig's memoir on the development of Asterina gibbosa. The various figures have, however, been enlarged or reduced as the case demanded so as to bring them to one uniform scale of magnification, viz. 85 diameters.

FIG. 1.—A gastrula with wide blastopore. Stage A. This stage is reached on the second day.

FIG. 2.—A slightly older gastrula. The blastopore is commencing to be narrowed, and one of its lips is reflected over it.

FIG. 3.—A still older gastrula.

FIG. 4.—Lateral view of larva three days old which has just escaped from the egg membrane. The "larval organ" (*l. o.*) or præoral ridge of ectoderm with long cilia has appeared. Stage B.

FIG. 5.—Ventral view of the same larva.

FIG. 6.—Dorsal view of the same larva.

FIG. 7.—Lateral view of larva of six days. The disc for adhesion (*fix.*) has appeared in the centre of the larval organ. Stage C.

FIG. 8.—Antero-lateral view of the same larva of six days.

Fɪɢ. 9.—Anterior view of the same larva of six days.

Fɪɢ. 10.—Left view of fully developed larva of seven days. Stage D.

Fɪɢ. 11.—The same drawn in the position it assumes in life.

Fɪɢ. 12.—Left view of larva in which metamorphosis has commenced, and which has fixed itself. The Arabic figures denote the primary lobes of the water-vascular system or hydrocœle, the Roman figures the rudiments of the arms. The larval organ has disappeared. Stage E.

Fɪɢ. 13.—Right view of the same larva.

Fɪɢ. 14.—Ventral view of larva of about nine days. The arm rudiments form a nearly complete circle. The lobes of the water-vascular system have developed two pairs of accessory lobes each. Stage F.

Fɪɢ. 15.—Right view of the same larva of about nine days.

Fɪɢ. 16.—Left view of the same larva of about nine days.

Fɪɢ. 17.—Oral view of just metamorphosed star-fish about ten days old. *amb.* Ambulacral ossicles. Stage G.

Fɪɢ. 18.—Aboral view of another specimen of the same age. *C.* Central plate. *B.* Basal. *T.* Terminal. The curve of the arm rudiments has become a circle, No. V coming to be apposed to the lobe No. 1 of the water-vascular system. *mp.* Madreporic pore. Stage G.

Fɪɢ. 19.—Aboral view of a young star-fish sixteen days old. Notice the anus, the additional calcareous plates, and the spines.

PLATE XII.

All the sections represented in this plate are magnified 80 diameters, and, except where otherwise stated, they have been cut parallel to the "larval plane," i.e. they are horizontal longitudinal sections. Where several sections from the same series are figured, the most dorsal is in every case put first. The darkest shade represents the epithelium of the gut; the intermediate shade represents ectodermic and cœlomic epithelium, including the lining of the derivatives of the cœlom; the lightest shade represents the cavity of the blastocœle with all its contained structures, jelly, fibres, cells, &c., and also the muscular tails of the epithelial cells lining the water-vascular system.

Fɪɢs. 20 and 21.—Two sections of a gastrula a little older than Stage A. No mesenchyme has as yet appeared.

Fɪɢ. 22.—Sagittal section of a gastrula about the same stage as Fig. 3. *mes.* Mesenchyme cells.

Fɪɢ. 23.—Section of an embryo older than that shown in Fig. 3. It shows the differentiation of the archenteron into gut and cœlom.

Fɪɢs. 24 and 25.—Two sections of an embryo somewhat younger than Stage B, and still enclosed in the vitelline membrane. The cœlom has grown back at each side of the gut, forming two posterior lobes, *lpc., rpc.* Fig. 25 shows, however, that these lobes do not as yet extend ventral to the gut.

Fig. 26.—Section of larva rather older than Stage B, to show the forma-
tion of the madreporic pore. *pc.* Pore-canal ending blindly in contact with
the ectoderm. *l. stom.* Larval stomach. *mp.* Thickening of ectoderm where
the primary madreporic pore will be formed.

Figs. 27—29.—Three sections of a larva slightly older than the preceding.
Fig. 27 shows that on the left side the cœlom is divided into an anterior
cœlom *a*, and a left posterior cœlom *lpc.* Fig. 28 shows that this division
only extends about halfway to the ventral side. Fig. 29 shows that the
separation of the cœlom from the archenteron commences ventrally, since here
the cœlom is shut off from the gut. *tr.* First trabecula.

Fig. 30.—Section of a larva rather older than that shown in Figs. 27—29.
lœ. Larval œsophagus. *tr.* Trabeculæ cords of cell spanning the left pos-
terior cœlom.

Fig. 31.—Sagittal section of larva about Stage B, to show the formation of
the larval œsophagus. It is clearly seen that this is a stomodæum which has
not as yet joined the gut.

Figs. 32—34.—Three sections of a larva younger than Stage C. The
segmentation of the cœlom on the left side is complete; on the right side it
has begun dorsally (Fig. 32). The left water-vascular rudiment or hydrocœle
(*lhy.*) has appeared as an outgrowth of the anterior cœlom, its lobes numbered
as in Pl. 18. Fig. 32 shows Nos. 1 and 2 ; Fig. 33, No. 3 ; and Fig. 34, Nos.
4 and 5.

Fig. 35.—Section of a larva of Stage C. The first trace of the right hydro-
cœle (*rhy.*) has appeared.

Fig. 36.—Section of a slightly older larva than preceding. The develop-
ment of the right hydrocœle is more advanced.

Figs. 37—41.—Five sections of a larva of Stage D, or slightly younger.
In Fig. 37 we see a section of the pore-canal (*pc.*) and the origin of the rudi-
ment of the oral cœlom (*or. c.*). In Fig. 38 the fully developed form of the
right hydrocœle (*rhy.*) is shown. In Figs. 39 and 40 we see the left posterior
cœlom extending obliquely beneath the right posterior cœlom (*rpc.*) ; this is
the right ventral horn (*l'p'c'.*) of the left posterior cœlom. In Fig. 41 we
see it opening into the anterior cœlom.

PLATE XIII.

The same remarks apply to this as to Plate 19, but in addition it is to be
remarked that the epithelium of the pore-canal and of the stone-canal is
distinguished by a cross-striation.

Figs. 42 and 43.—Two sections of a larva rather younger than Stage D.
stc. Rudiment of the stone-canal. Fig. 42 shows the septum between the
anterior cœlom and the left posterior cœlom broken down dorsally; and Fig.
43 shows that the septum between the anterior cœlom and the right posterior
cœlom is still incomplete ventrally.

FIGS. 44—46.—Three sections of a larva of Stage D. Fig. 44 shows the opening of the pore-canal into anterior cœlom; Fig. 45, opening of the stone-canal into the same; and Fig. 46, the opening of the stone-canal into the hydrocœle. It shows also that the hydrocœle has a wide opening into the anterior cœlom independent of the stone-canal.

FIG. 47.—Sagittal section of a larva of Stage D, to show the relations of the lobes of the left hydrocœle to each other.

FIGS. 48—50.—Three sections of a larva of Stage E. The larva has suffered an injury, a piece of ectoderm in the præoral lobe indicated by the dotted line being missing. Fig. 48 shows relation of rudiment of oral cœlom (*or. c.*) to the right dorsal horn of left posterior cœlom ($l''p''c''$.). Fig. 50 shows the great growth of the left hydrocœle (compare Fig. 40). *a. œ.* Adult œsophagus; rudiment of the "stomach" of the adult. In Fig. 49 the *o* of *or. c.* has failed to print.

FIGS. 51—53.—Three sections of a larva slightly older than the preceding, to show rudiments of the perihæmal spaces (*ph.*). These are numbered according to the lobes of the hydrocœle. between which they occur: *ph.* 1.2, *ph.* 2.3, *ph.* 3.4, and *ph.* 4.5. *ph.* 1.2 arises from the anterior cœlom, the rest from the left posterior cœlom. The lobes of the hydrocœle are commencing to be trifid.

PLATE XIV.

The same remarks apply to this plate as to the two foregoing.

FIGS. 54—57.—Four sections of a larva about midway between Stages E and F. Fig. 54 shows the incipient dorsal constriction of the anterior cœlom into a stalk portion (*a.*) and a body portion or axial sinus (*a'*.); also the origin of the perihæmal rudiment (*ph.* 1.2) from the anterior cœlom. Fig. 55 shows the growing tip of the right ventral horn of the left posterior cœlom, and over it the arm rudiment No. V; it shows also the stone-canal opening into the hydrocœle and the perihæmal rudiment insinuating itself between the hydrocœle and the ectoderm. Fig. 56 shows the axial sinus and the stalk cœlom continuous with each other, and also the anterior cœlom opening into the right ventral horn of the left posterior cœlom. Fig. 57 shows that this right ventral horn is commencing to be again divided from the anterior cœlom ventrally by the outgrowth of a septum.

FIGS. 58 and 59.—Two sections of a larva slightly older than the preceding, to show the separation of the axial sinus ventrally on the one hand from the stalk cœlom, and on the other hand from the hydrocœle. *Py.* Rudiment of the pyloric sac of adult. *lœ.* Last trace of the larval œsophagus.

FIG. 60.—Section of larva about the same age as preceding, to show the fifth perihæmal rudiment (*ph.* 51) which intervenes between lobes 5 and 1, as yet widely separated.

FIG. 61.—Section of larva about Stage F, to show the mutual relations of the stone-canal, the axial sinus (*a'*.), the right dorsal horn of the left posterior cœlom (*l''p''c''*.), and the right hydrocœle (*rhy*.).

FIGS. 62—69.—Eight sections of a larva slightly older than Stage F, to show the relation of the arm rudiments to the lobes of the hydrocœle. Fig. 63 shows the incipient healing of the breach in the septum between the anterior cœlom (axial sinus) and the left posterior cœlom. Figs. 64 and 65 show that arm rudiment No. V is still widely separated from hydrocœle lobe 1 by the base of the stalk, and also that the right ventral horn (*l'p'c'*.) of the left posterior cœlom is not completely separated from the axial sinus (*a'*.). Fig. 65 also shows the complete separation of the hydrocœle from the axial sinus. Figs. 66 and 67 show relation of the oral cœlom (*or. c.*) to the adult œsophagus (*a. œ.*). Fig. 69 shows the adhesive disc of the stalk (*fix.*) attached to a piece of Alga (*x*), and the rest of the ectoderm of the præoral lobe being invaginated (*hist.*) to undergo destruction. It also shows that each primary lobe of the hydrocœle has developed two pairs of secondary lobes.

PLATE XV.

The same remarks apply to Figs. 70—78 as to the contents of the three foregoing plates. Figs. 79—82 are sections cut parallel to the disc of the star-fish or "adult plane," the magnification being the same, viz. 80 diameters.

FIGS. 70 and 71.—Two sections of a larva of Stage G. Fig. 70 shows the relationship which the adult and the larval œsophagus occupy with regard to one another, the latter being a mere rudiment unconnected with the gut; it also shows the outgrowths from the adult œsophagus. Fig. 71 shows the oral cœlom opening into left posterior cœlom ventrally by breaking down of the partition between them; also the first trace of the pyloric cæca as outgrowths from the pyloric sac.

FIG. 72.—Section of larva rather older than Stage G. The adult mouth is formed, and the oral cœlom opens widely into the left posterior cœlom. The stalk has become a small solid rudiment. The dotted line shows the boundary between the pyloric sac and the adult " œsophagus " or " stomach."

FIG. 73.—Section of a larva of the same age as the preceding ; it shows the two dorsal pyloric cæca already formed, also the so-called heart or " ovoid gland " (*ovg.*), as a fold projecting into the axial sinus (*a'*.).

FIG. 74.—Another section from the same series as Fig. 72. Shows the two ventral pyloric cæca; it is seen also that their suspensory mesenteries are derived from the mesentery separating the right posterior cœlom from the left (compare Fig. 75). Note also that the tube-feet have acquired their suckers. The animal has broken loose from its attachment, which accounts for the rudimentary condition of the stalk.

FIG. 75.—A section of a larva of Stage G. Shows the dorsal pyloric cæca and their suspensory mesenteries.

FIG. 76.—A section of another larva of Stage G. Compare with Pl. IV, fig. 61, and note that the arm rudiment No. V (not marked in the figure) has now become applied to the lobe No. 1 of the hydrocœle. The stone-canal is seen opening into lobe No. 2, and the perihæmal rudiment 1.2 has grown out into a canal insinuating itself between the ectoderm and the hydrocœle.

FIGS. 77 and 78.—Two sections of a rather older larva. Fig. 77 shows that the right ventral and right dorsal horns ($l'p'c'$. and $l''p''c''$.) of the left posterior cœlom have coalesced, and that the left posterior cœlom has thus acquired a ring-like form. Fig. 78 shows the formation of the anus of the adult.

FIG. 79.—Section parallel to the adult plane of a larva of Stage F. Shows the relationships of the axial sinus, oral cœlom, and water-vascular ring (*wvr.*), the last being still incomplete; also four perihæmal rudiments alternating with the five hydrocœle lobes.

FIGS. 80 and 81.—Two sections in same plane as Fig. 79 of a larva of Stage G. Fig. 80 shows the axial sinus (a'.) in process of growth to form the inner perihæmal canal. Fig. 81 shows the completion of the water-vascular ring at the spot marked by the asterisk between the hydrocœle lobes Nos. 1 and 5; it also shows the trifid form of the adult œsophagus before the mouth is formed, and the oral cœlom opening into the left posterior cœlom.

FIG. 82.—Similar section of older larva in which mouth is formed. The five interradial lobes of the "stomach" are present, the trifid shape having disappeared; and the retractor muscles of these lobes are formed from remnants of septum between oral and left posterior cœlom. The distance (R) from tip of arm to centre of disc ·36 millimetre.

PLATE XVI.

FIGS. 83 and 84.—Two more sections from the same series as Fig. 82. Fig. 83 shows the pyloric sac with its five cæca just beginning to be bifid, and the mutual relations of the right hydrocœle and axial sinus; also the stone-canal opening into the latter. Fig. 84 shows the point of origin of the rectum and the rudiment of rectal cæcum and the relation of right posterior cœlom to the pyloric cæca. In Fig. 83 (*pr. germ. inv.*) is the involution of peritoneum from which the primitive germ cells are formed.

FIGS. 85—94 represent sections of abnormal larvæ. These sections are cut parallel to the larval plane, except Fig. 90, which is rather oblique to that plane. Magnification the same as before.

FIGS. 85 and 86.—Two sections of a larva of Stage D, or slightly younger. *rhy*. Right hydrocœle developed into two distinct lobes lined with cubical epithelium.

Figs. 87 and 88. Two sections of a larva between Stages D and E. *p'c'.*, *st'c'.* Pore-canal and stone-canal of right side in connection with normal right hydrocœle, *r. hy.* Their openings into this are in another section. *r'hy'.* A second; more ventrally situated hydrocœle rudiment on the right side, with a distinct opening into cœlom. The left hydrocœle is feebly developed for the stage which the larva has reached, and has only four lobes.

Fig. 89. Section of a larva of Stage D, in which the right hydrocœle has five lobes, and is larger than the left. This section is drawn from the ventral aspect, and hence appears reversed.

Fig. 90. Section of a larva of Stage G, showing a "collar pore" opening from the left hydrocœle between lobes 2 and 3, directly to the exterior.

Figs. 91—94. Four sections of an almost normal larva of Stage F, or somewhat older. *p. c.* Normal pore-canal, opening into axial sinus, the septum between the latter and the left posterior cœlom being still incomplete dorsally. *p'. c'.* Pore-canal, *st'. c'.*, and stone-canal in connection with the right hydrocœle. Fig. 93 shows the opening of the second pore-canal into the axial sinus. Fig. 92 shows the opening of the second stone-canal into the right hydrocœle. Fig. 91 shows the two pore-canals uniting to open by a common pore. (Compare Woodcut 3.)

FIG. 95.—Section parallel to the larval plane from larva of Stage C, showing the first trace of right hydrocœle. (Compare Plate 19, fig. 35.) Note its relationship to the anterior cœlom, which extends obliquely beyond it posteriorly, passing under it and to the right of it. Magnification 1000 diameters; Leitz's immersion $\frac{1}{12}$.

FIGS. 96 and 97.—Two sections of body-wall of young star-fish, cut perpendicular to disc, in which R equals ·8 millimetre. Fig. 97 shows first trace of "papula" or dermal branchia (*branch.*). Fig. 96, origin of its peribranchial space, *p.br.* Magnification 400 diameters.

FIG. 98.—Section of body-wall of young star-fish, in which R equals ·88 millimetre, showing dermal branchia and its peribranchial space. Magnification about 400 diameters.

PLATE XVII.

FIGS. 99—106 illustrate the development of the so-called heart or "ovoid gland." The sections represented are perpendicular, or nearly so, to the disc of the star-fish, and the magnification is 350 diameters.

Fig. 99. Section of larva of Stage G. *ov.g.* Fold projecting into the axial sinus, the rudiment of the ovoid gland. *pr. germ. inv.* Invagination of peritoneum, whence the primitive germ cells are formed. *Calc.* Calcigenous tissue in the body wall.

Figs. 100—103. Four sections of a specimen older than preceding. Fig. 101 shows the growth of the primitive germ cells into the rudiment

of the ovoid gland. Figs. 102 and 103 show that they do not yet extend through its whole extent. Fig. 103 shows that the ovoid gland rudiment is at one point attached to the oral wall of the axial sinus. (Compare Plate 25, fig. 110.)

Figs. 104—106. Three sections of a young star-fish, in which R equals ·4 millimetre. Fig. 104 shows the primitive germ cells arising from the involution of the peritoneum. Figs. 105 and 106 show that they now extend throughout the whole extent of the ovoid gland; these figures also show the relation of the oral end of the axial sinus to the perihæmal spaces.

Figs. 107 and 108.—Two sections from same series as Figs. 82—84, magnified 350 diameters. They show the development of the oral "blood" ring, *sang. circ.*, as a modification of the mesenchymatous tissue of the blastocœle. *fibr.* Fibrous tissue.

Fig. 109.—Similar section of a young star-fish, in which R equals ·45 millimetre. Same magnification. The blood-ring is fully formed. Notice also the minute cells amongst the nerve-fibres (*bip. gang.*).

PLATE XVIII.

Fig. 110.—Longitudinal section of the stone-canal of young star-fish, in which R equals ·8 millimetre. *sang. circ.* Oral "blood" ring. *wvr.* Watervascular ring-canal. *musc. amb.* Muscles of ambulacral ossicles. Notice the incipient division of madreporic pore into two, and entire independence of ovoid gland and blood-ring. Magnified 350 diameters.

Fig. 111.—Diagram showing the relative positions of the ovoid gland, stone-canal, and various sinuses in proximity. *gen. r.* Genital rachis. *ab.* Aboral sinus (or *sinus a.*). *pr. germ. inv.* Primary peritoneal involution to form germ cells. The cavity of this is probably the same as *sinus b* in next figure. The axial *sinus a'* is *sinus c.* The dotted lines show the continuity of two parts of the ovoid gland in a different plane to that of the stone-canal.

Fig. 112.—Similar diagram of Amphiura squamata. Accompanying spaces, *sinus a, sinus b,* and *sinus c,* as in the author's paper (14).

Figs. 113—118 illustrate the development of the ovoid gland and genital rachis. They are all taken from sections cut parallel to the disc; they are, in fact, transverse sections of the interradial septum in which the axial sinus is embedded.

Figs. 113 and 114. Two sections from a star-fish, in which R equals ·45 millimetre. Fig. 113 shows the manner in which the right hydrocœle is enclosed in the upper part of ovoid gland; Fig. 114, the primitive peritoneal involution, the pore-canal, and the crescentic form of right hydrocœle. Magnification 350 diameters.

Figs. 115 and 116. Two sections from star-fish, in which R equals ·7 millimetre. *ab.* Aboral sinus containing the rudiment of genital

rachis. Fig. 115 shows that the sinus is a portion of the cœlom shut off by the outgrowth of a flap from the body-wall.

Fig. 117. Section from star-fish, in which R equals 2·2 millimetres, showing the continuity of rachis and ovoid gland, and that the rachis now extends in both directions. Magnified 150 diameters.

Fig. 118. Section from star-fish, in which R equals 3 millimetres, showing fully developed ovoid gland and changed form of stone-canal. Magnified 350 diameters.

PLATE XIX.

Figs. 119—121.—Portions of three sections from the same series as Fig. 118. Fig. 119 shows the genital rachis enclosed in the branch from the aboral sinus, *ab*. Fig. 120 shows the passage of the genital rachis into the rudimentary genital organ, and the outgrowth of septum which cuts off the perihæmal space surrounding this rudiment from the "genital vessel." *ab*. A branch of the aboral ring. Fig. 121 shows the development of the cavity of the genital organ. Magnification 350 diameters.

Figs. 122 and 123.—Two sections of young ovaries, from a specimen in which R equals 3·7 millimetres. Fig. 122 shows the continuity of the ovary and rachis, Fig. 123 the outgrowth of germ cells to form the genital duct.

Fig. 124.—Portion of body-wall of gastrula figured in Plate 19, fig. 21. Notice the absence of mesenchyme. *end.* Endoderm. Magnification 600 diameters.

Fig. 125.—Similar view of the body-wall of slightly older embryo, to show the formation of mesenchyme. Same magnification.

Fig. 126.—Portion· of the gut epithelium of larva figured in Plate 20, figs. 51—53. Same magnification.

Fig. 127.—Epithelium of the adult œsophagus of the larva shown in Plate 22, fig. 76, Stage G. Magnified 480 diameters.

Fig. 128.—Epithelium of the pyloric sac (larval stomach), from the same section as foregoing.

Fig. 129.—Epithelium of the lateral wall of the stomach of a star-fish, in which R equals ·8 millimetre. Magnified 480 diameters.

Fig. 130.—Epithelium of aboral wall of the stomach from the same section as foregoing. At × it passes into the epithelium of the pyloric sac.

Figs. 131 and 132.—Epithelium of the pyloric sac and of the rectal cæcum respectively. From the same section as fig. 130.

PLATE XX.

Figs. 133—135.—Three sections of the ectoderm of the anterior surface of præoral lobe of larva of Stage D. *Fix.* Disc for fixation. *l. o.* Larval

organ. *nerv. larv.* Larval nervous tissue. Fig. 133 is through the dorsal part of præoral lobe; Fig. 135 through its ventral tip. Magnified 480 diameters.

FIG. 136.—Section of the adhesive disc of larva shown in Plate 21, figs. 62—69. *x.* A small piece of alga, to which it adheres by a secretion of mucus. *hist.* Involutions of neighbouring portions of ectoderm to undergo destruction by amœbocytes, *amœb.*; by this means the præoral lobe is reduced in size. Magnified 480 diameters.

FIG. 137.—Section of the lateral wall of præoral lobe of larva of Stage D. *musc. larv.* Larval muscles derived from the peritoneal cells. Magnified 1000 diameters.

FIG. 138.—Section through the ectoderm and hydrocœle wall of a larva of Stage D, to show the characters of the various larval epithelia. Magnified 1000 diameters.

FIG. 139.—Similar section from a larva between Stages E and F. A peri-hæmal rudiment is shown. Magnified 1000 diameters.

PLATE XXI.

FIGS. 143, 149, and 150 are magnified 600 diameters, the rest 1000 diameters (Leitz's immersion $\frac{1}{12}$).

FIG. 140.—Similar section from a larva of Stage F (that shown in Figs. 62—69). *nerv.* The incipient nervous tissue developing as a fine plexus amidst the bases of the ectoderm cells.

FIG. 141.—Similar section from a young star-fish, in which R equals ·4 millimetre. *Nerv. circ.* Nervous ring. *calc.* Calcigenous tissue. *fibr.* Fibrous tissue. *retr. musc.* Retractor muscles of stomach.

FIG. 142.—Developing eye of same star-fish. A simple ectodermic pit is seen.

FIG. 143.—Eye of star-fish from which Figs. 129—132 are taken. *ret.* Visual cells. *vit.* Cells functioning as "Glaskörper."

FIGS. 144—148 illustrate the differentiation of tissues in the body-wall.

Fig. 144. From the right side of a larva of Stage D. At * a cell is seen in the act of dividing, to form one of the amœbocytes of the cœlom.

Fig. 145. From larva of Stage E (that shown in Figs. 51—53). *gob.* Goblet cells. *musc.* Developing muscles; as yet they are simply tails of the cœlomic epithelium. *fibr.* First rudiment of the fibrous tissue.

Fig. 146. From the young star-fish from which Fig. 141 is taken. *calc.* Small portion of calcigenous tissue.

Fig. 147. From the young star-fish from which Fig. 143 is taken, and also Figs. 129—132.

Fig. 148. Ectoderm of another specimen of same age, to show the sense-cells.

FIG. 149.—Tube-foot of the larva shown in Figs. 62—69.

FIG. 150.—Tube-foot of the star-fish from which Figs. 141 and 146 are taken. *nerv.* Nervous tissue under the sensory epithelium at the tip. *musc.* Muscular tails of hydrocœle epithelial cells.

PLATE XXII.

FIGS. 151—154 show the development of the transverse muscles, which extend from one ambulacral ossicle to its fellow of the opposite side.

> Figs. 151 and 152.—Two sections perpendicular to the disc from a star-fish, in which R equals ·4 millimetre. *sang. circ.* Oral "blood" ring. *musc. amb.* Ambulacral muscles. *ph.* Perihæmal space. Magnified 350 diameters.
>
> Fig. 153. Similar section from star-fish in which R equals ·63 millimetre.
>
> Fig. 154. Similar section from star-fish of the same size as the preceding, but more advanced in the development.

FIG. 155.—Transverse section of the radial nerve-cord of a young Asterias, to show the feeble development of cœlomic nervous system.

FIG. 156.—Similar section of nerve-cord of an Ophiurid, to show the great ganglia of the cœlomic nervous system.

FIG. 157.—Diagram of the hypothetical ancestor of Asterids and Crinoids. The hydrocœle is a paired structure.

FIG. 158.—Diagram of a stage in the evolution of Asterids from this ancestor. Notice the growth of both left hydrocœle and left posterior cœlom to form rings. The hydrocœle encircles the base of the stalk. This drawing does not properly represent the oblique position which the disc acquires in reference to the stalk. The mouth ought to be half turned towards the observer.

FIG. 159.—Diagram of stage in evolution of Crinoids. Notice that the hydrocœle is carried entirely away from the stalk.

These last two diagrams are only hypothetical, in so far as they represent as co-existing structures which succeed one another in ontogeny; otherwise they represent the actual fixed stage in both Asterid and Crinoid ontogeny.

blastopore.

1   2   3   4

A

lo.

C

fix

lo

(pr

8   9   10

F

stalk.

5   5   1

V   I   V   5   2

4   II.   4   IV.   4

IV.   III.   stalk.   3

III.   14   15   16

amb   stalk.

5   1   V   5

mp   T   B   IV

4   2   B   T

G   B   C   B

2   I T   T

3   4   B   III

17   3   18

lo.

blastopore.
(larval anus).

5

6

B

fix

7

C

lo.

oral lobe)

D

11

stalk.
(praeoral lobe).

V.

5   1

4   2

3

IV

I.

II.

III.

12

E

anus

np

1

5

2

4

3

19

I.

V.

IV.

III.

13

archenteron

20

blastopore

21

mes.

22

a

pc
m p
l. stom.

26

a

lpc
rpc

27

a

lpc
tr
rpc

28

a

lhy
1
2
lpc.
rpc

82

a

loe
lhy
tr

83

loe
lhy
a
5

8

a

2
lhy
a
pc
or.c
lpc
rpc

87

a

rhy.
lhy
or.c
5

88

lhy
3
a
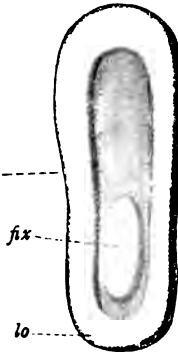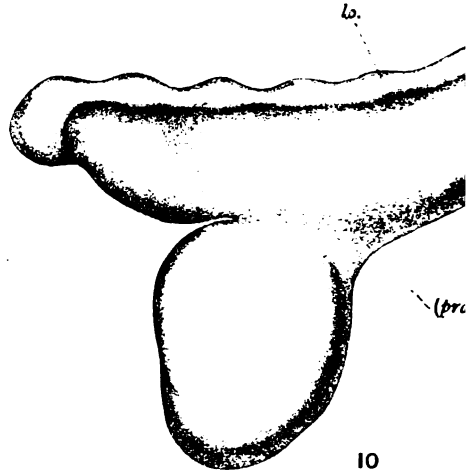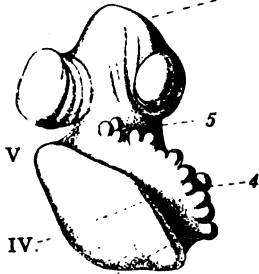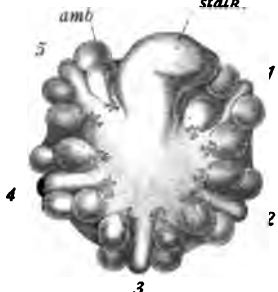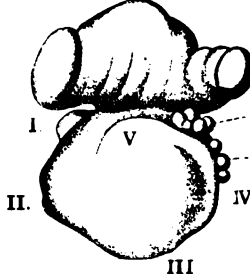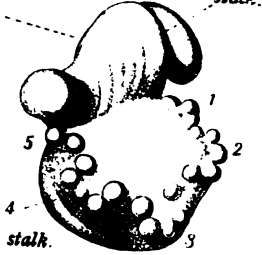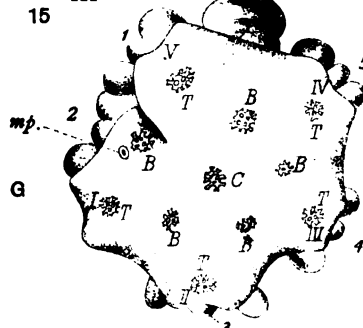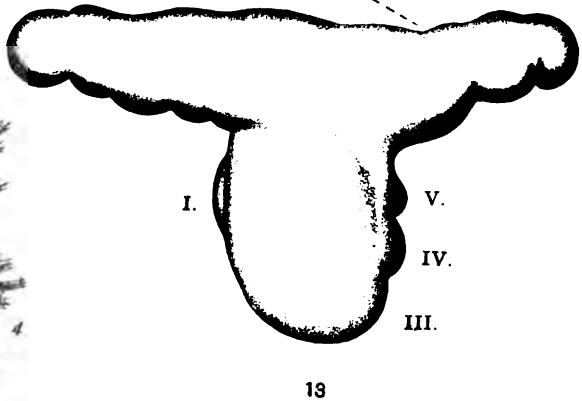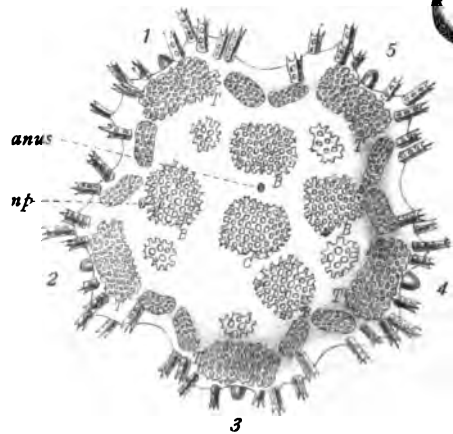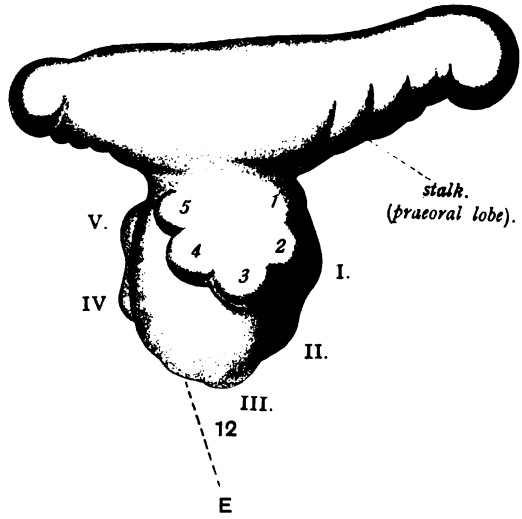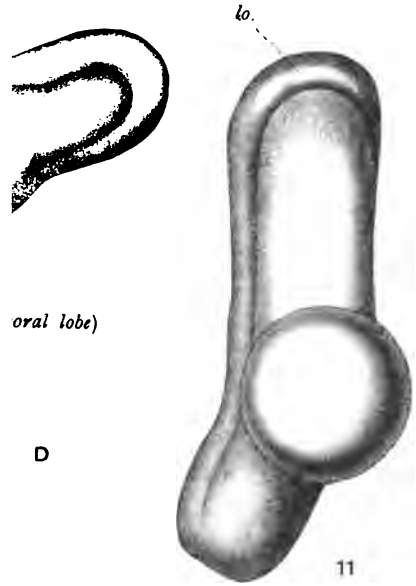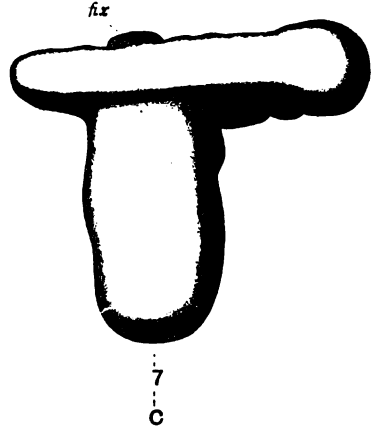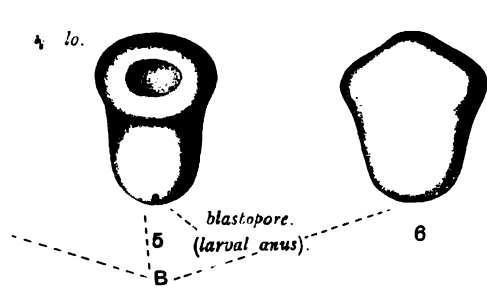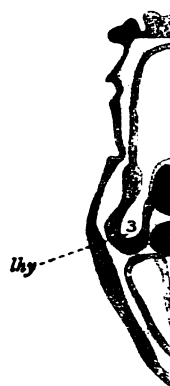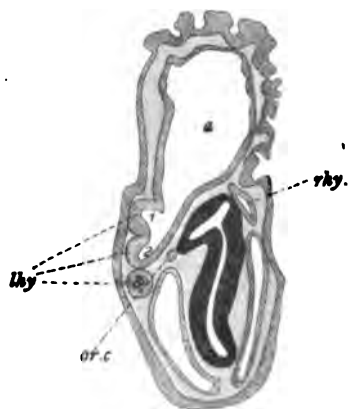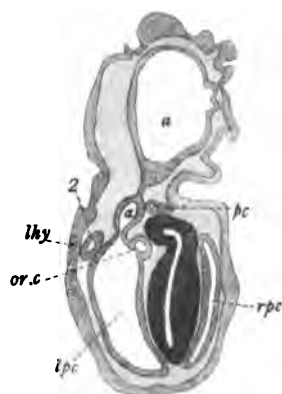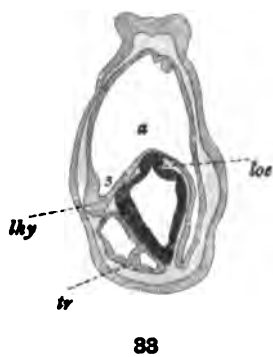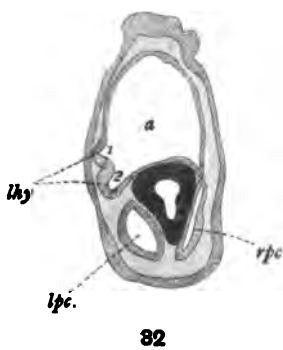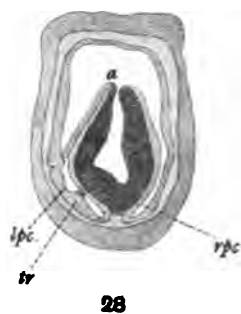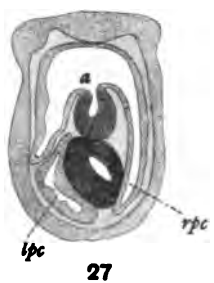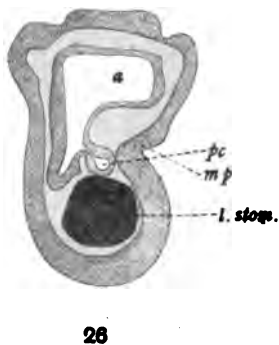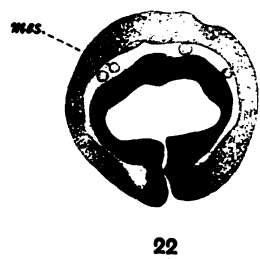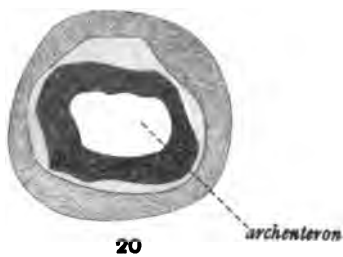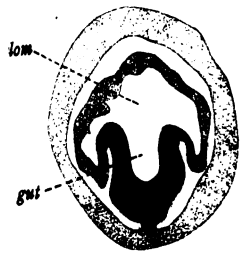
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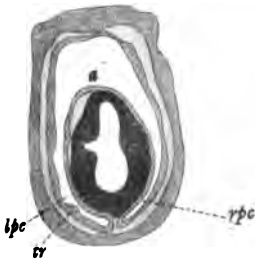
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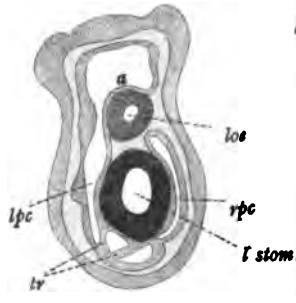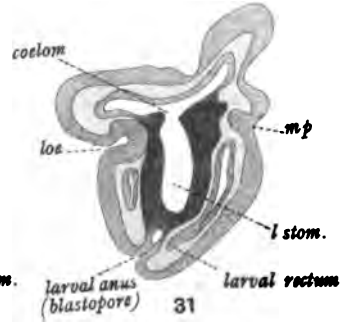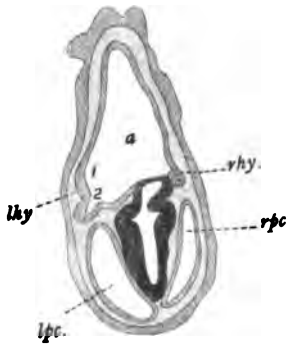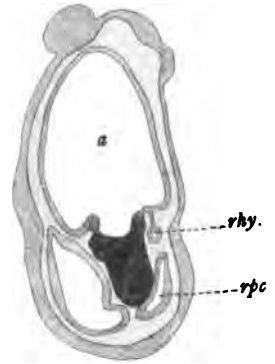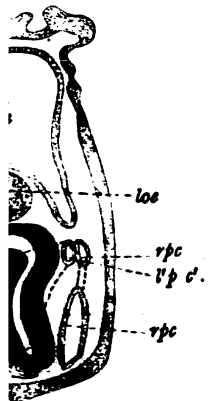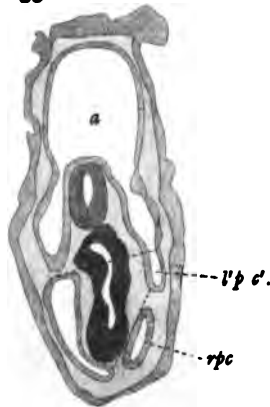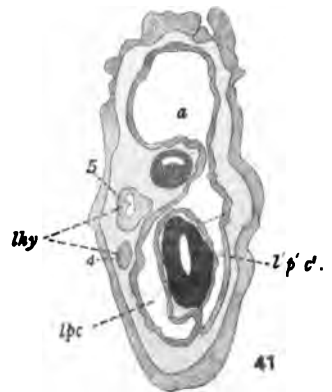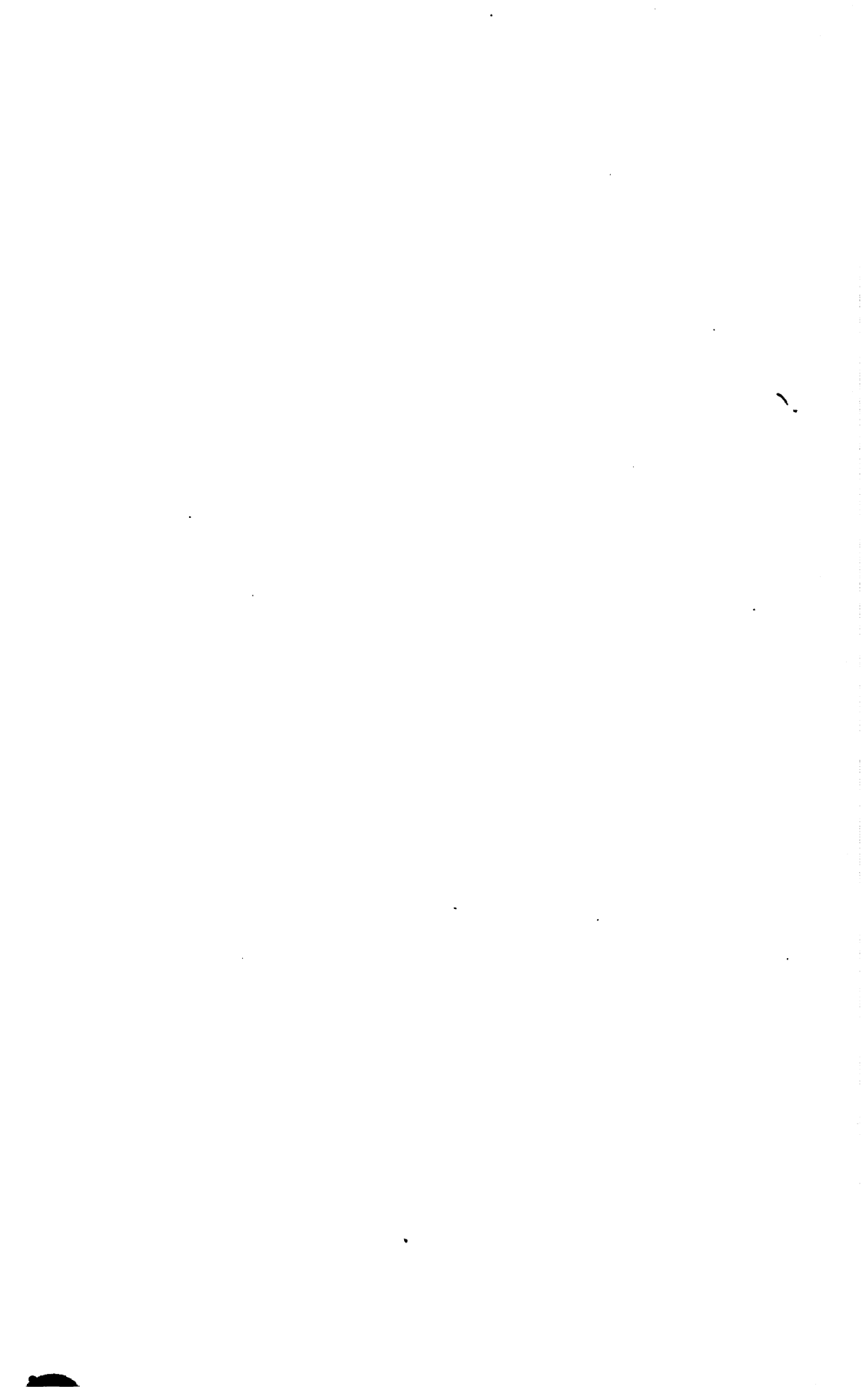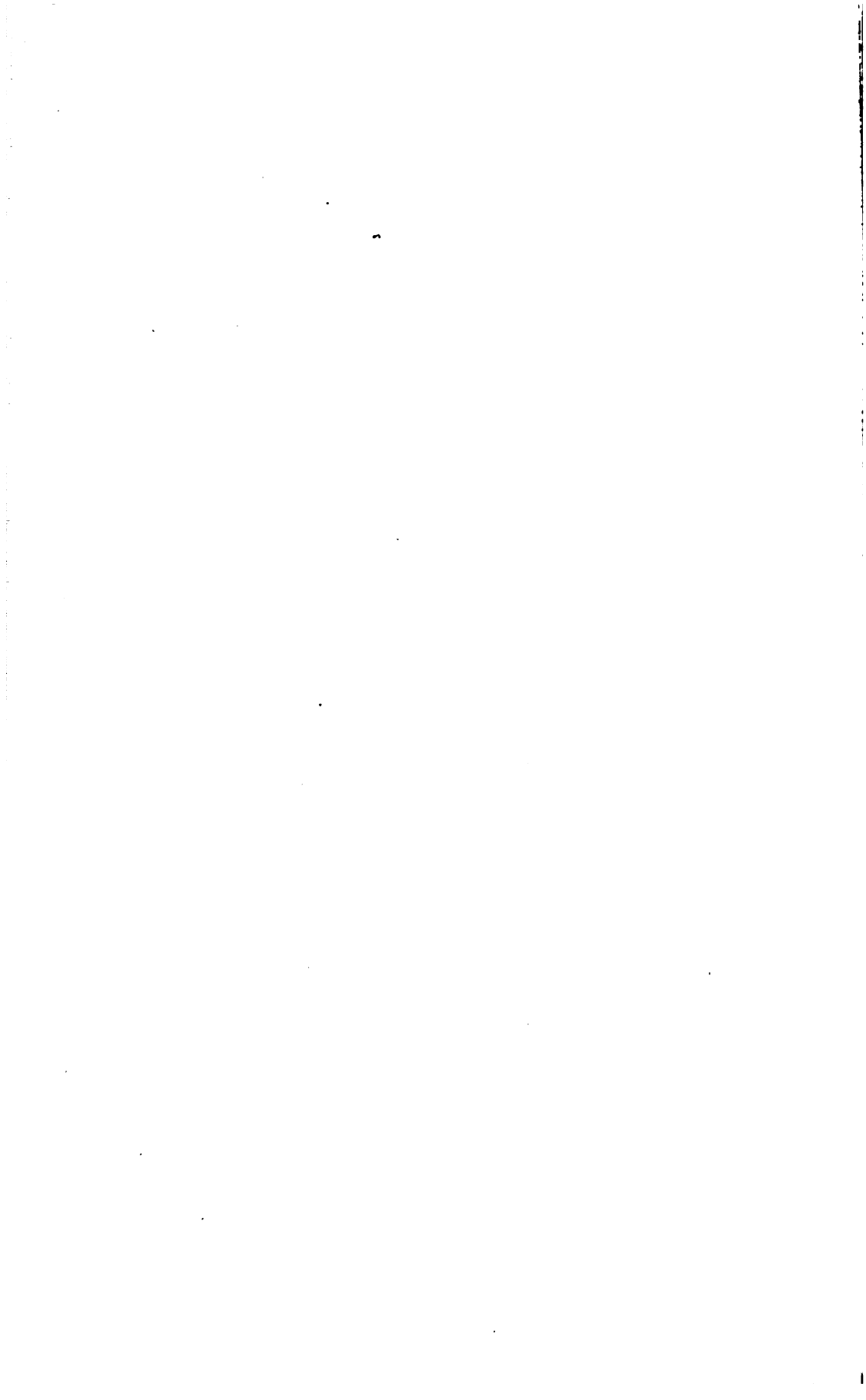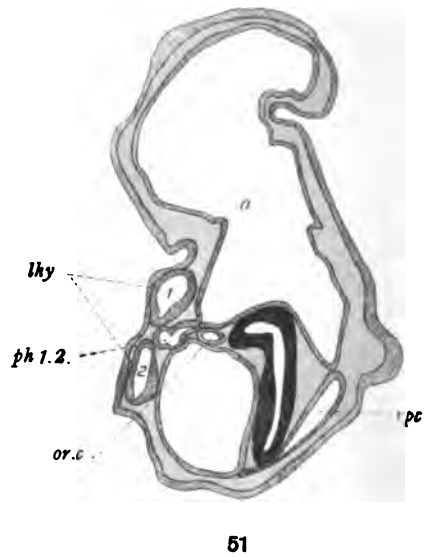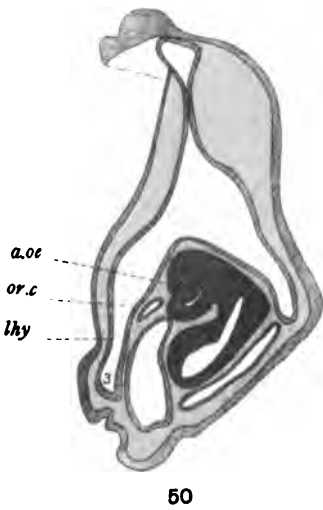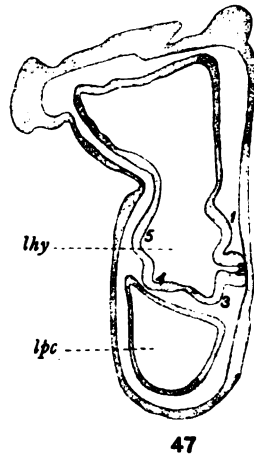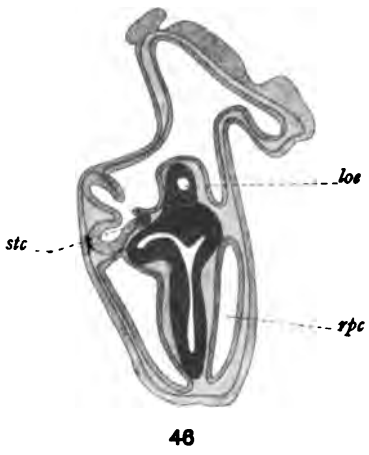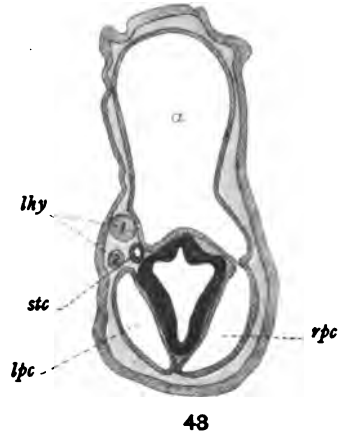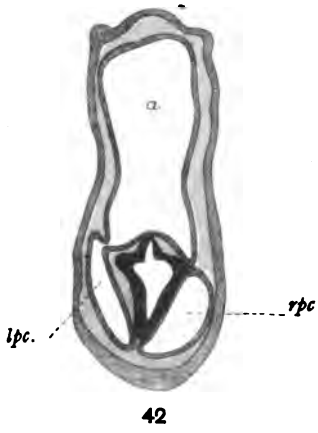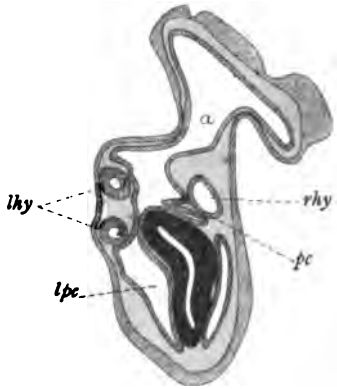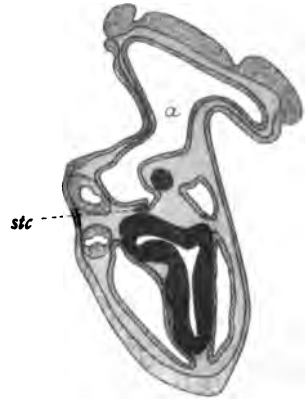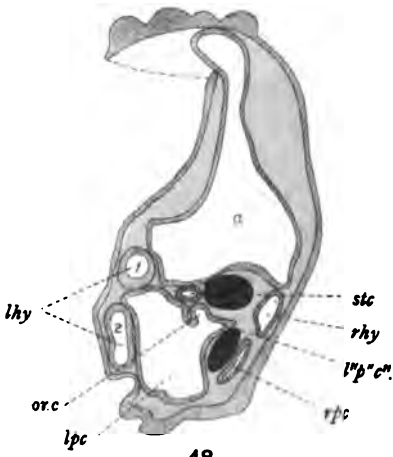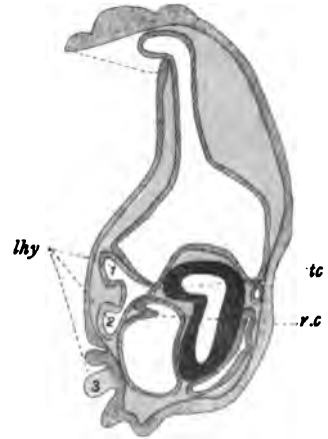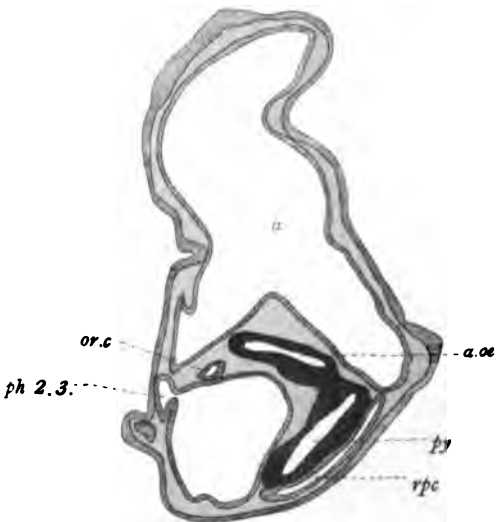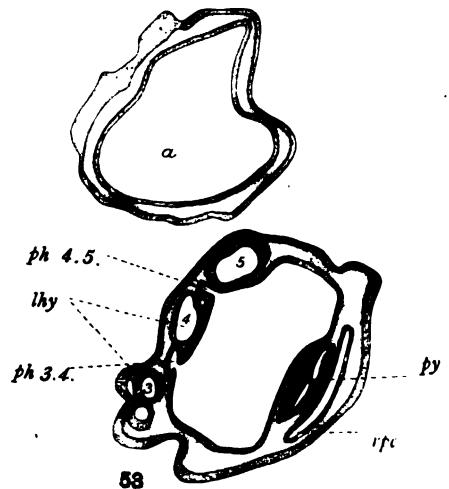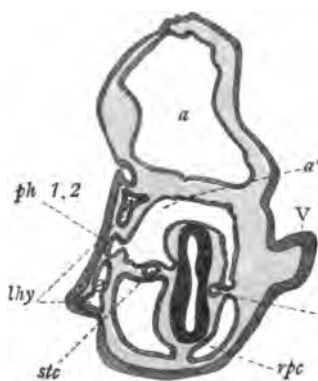
54   55   56

60   61

64   65   66

57

58

59

stalk.

62

63

III.   67

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76
79
80

72

78

74

77

78

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82

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84

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88

91

92

95

96

gut wall

rhy

a

a

py

il coecum

85

86

89

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93

94

97

98

Figure 99

Figure 100

Figure 104

Figure 108

Figure 107

101

102

106

108

109

ASTERINA.

110

111

114

116

117

AMPHIURA

sinus b

pr. germ

sinus a

inv us b)

env

sinus c

stc

sinus b'

pc

112

pr germ

stc

rhy

ovg

a'

113

ab

pr. germ inv.

gen.r

rhy.

stc

a'

115

stc

stone canal

ovg

a'

pr. germ

118

119

gen.r

septum

ai

gonad

120

ab

gen v

duct

ab gon

ab gon

123

124

127

128

gla

129

121

122

126

125

130

131

132

133

nerv. larv.

fis

lo

ne

x

ect

amoeb

hist

136

ect

134

135

nerv. larv.

). larv.

ect

amoeb

per

musc larv.

137

lhy 5

lhy 4

139

ph 4 5

per

138

ph 1.2

nerv

per

lhy.1

140

musc retr

calc

wo 2

ph

141

sense cells

148

per

mes.

144

gub

fibr

amoeb

145

per

fibr

ph

inv   142

nerv

ret

vit

143

fibr   amoeb

nerv. circ

ect

sense cells

calc

musc

amoeb

fibr

146

147

musc

calc

gob

nerv.

149

150   musc.

151

152

153

sang. circ

nerv. circ

musc. amb.

musc. amb.

ph

sang. circ

musc. amb.

ph

sang. circ

ph

musc. amb

vv

ph

ph

coelomic nervous system

subneural

OPHIURID.

156

anus

mp.

mouth

157

wv

wv

ph

wv

ph

nusc
amb.

ph

ph

154

----coelomic
nervous system.

ASTERID.

155

----mouth

---ace

---anus
---mp.

mp.

----a

----anus

mouth

----a

59

158

VB571